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# ALGAL-BEARING DIDEMNID ASCIDIANS IN THE INDO-WEST-PACIFIC

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ABSTRACT

New material from the fringing reefs of Viti Levu and from the Great Barrier Reef form the basis for a review of the taxonomy, phylogeny, habitat, distribution and larvae of 18 species of the family Didemnidae displaying symbiosis with prokaryotic algae. The species are in the genera *Didemnum, Tridemnum, Lissoclinum Echinoclinum* and *Diplosoma*, and include two new species, one of which is endemic and probably isolated in an unusual habitat on the southwestern fringing reefs of Viti Levu.

A remarkable organ for the transference of algal cells from generation to generation in *Diplosoma* spp. is described for the first time. The name *rastrum*, or plant rake, is proposed for this organ.

The mechanism for gene flow in species with a wide range between 30°N and 30°S latitude, and 30°W and 150°E longitude is discussed.

Nine algal-bearing Ascidiacea of the family Didemnidae from the Great Barrier Reef, were formerly reported by Kott (1977). The present paper discusses these and a further 9 species, and represents a review of all the known Pacific Ocean ascidian species that display an intimate association with blue-green algae. A large quantity of material from a wide range of locations (including the larvae and the types of most of the species) has been examined. It has been possible to resolve much of the confusion relating to the identity and synonymy of this interesting, albeit neglected, group of didemnid ascidians.

The species in which plant cells are known to occur are in 5 genera (viz. *Didemnum, Tridemnum, Lissoclinum, Echinoclinum* and *Diplosoma)*. The relationship does not appear to have evolved in the two remaining genera of the family *(Leptoclinides* and *Polysyncraton)*.

The view that the relationship between plant cells and host is symbiotic is supported by the presence of peculiar adaptations for the transferance of plant cells to the next generation in the 15 species for which larvae are known. In the genus *Didemnum* the larva is known only for *D. molle* and its mechanism for carriage of plant cells is similar to that in *Lissoclinum* spp. *Tridemnum* spp. have different mechanisms; and in *Diplosoma* spp. a unique and previously undescribed organ, the *rastrum* or plant-rake is present (see *D. virens,* below).

In some cases the similarity between these larval adaptations for carriage of plant cells tends to support the view that there are close phylogenetic relationships between groups of species in each of the genera represented. Studies of the plant cells could provide further evidence in this regard. However, the fact that the ascidian/plant cell relationship appears to have evolved separately, and sometimes more than once, in each genus further supports the view that some mutual advantage is derived from the association. The ascidian colony at least provides a habitat for the algae, but it is not known what adaptive advantage is conferred on the ascidian colony by the algae. It should not be overlooked, however, that while other ascidians (including didemnid species) invariably occupy more cryptic habitats in the rubble zone behind the reef crest or in caves and crevices in deeper waters down the slope, certain of these plant-bearing species are extremely common on the reef flat where they are exposed to great light intensity *(Diplosoma* spp. and *Lissoclinum voeltzkowi)*. There is a latitudinal gradient in the occurrence of these reef flat species that may result from increasing diurnal temperature range to the south, but may also be affected by light. Olsen (1979) has shown that colonies of *T. cyanophorum* do not grow in the absence of light.

Much of the new material that comprises the basis of this report is from the reef flats of the fringing reefs of Viti Levu. Material from the Great Barrier Reef (Lizard I. and Green I. in the north; Townsville in the central section; and Heron I. in the south) supplements the Fijian collections. Of the wide ranging species in the region, only *Didemnum molle* (> *D. ternatanum:* Kott, 1977) and *Lissoclinum patellum* were not taken from the Fijian reefs. These two species are more often found on the reef slope at a wide range of locations in the Indo-west-Pacific. When deeper waters are sampled, they may be found in the Fijian waters. Only a single new species of *Tridemnum* appears to be endemic in Great Barrier Reef waters. A few endemic species of more restricted range occur but are a relatively rare phenomenon. A new species of *Diplosoma* from Fiji, two new species of *Tridemnum* from the Philippines, and *Diplosoma handi* (Eldredge) from the Caroline Is. are the only plant bearing didemnids that appear to be endemic. It is apparent that there is some strategy available to most species that will ensure gene flow over a wide geographic area.

Although didemnid/algal symbiosis was not thought to occur in the Atlantic Ocean (Kott 1977) it is now known in *Tridemnum cyanophorum* Lafargue and Duclaux, 1979, which occurs in profusion in shallow water coralline habitats off Panama and Guadaloupe. In this large investing species the algal cells are found embedded in the superficial layer of test and not in the common cloaca.

ABBREVIATIONS: The following abbreviations are used below: AM Australian Museum, Sydney; AMNH American Museum of Natural History, New York; AMPI Australian Marine Photographic Index; BM British Museum (Natural History), London; QM Queensland Museum, Brisbane, Australia; USNM United States National Museum, Washington D.C.; ZMA Zoological Museum, Amsterdam; ZMH Zoologischen Staatsinstitut und Zoologischen Museum, Hamburg.

**Didemnum molle** (Herdman, 1886)
(Figs 1, 2; Plate 1·1)

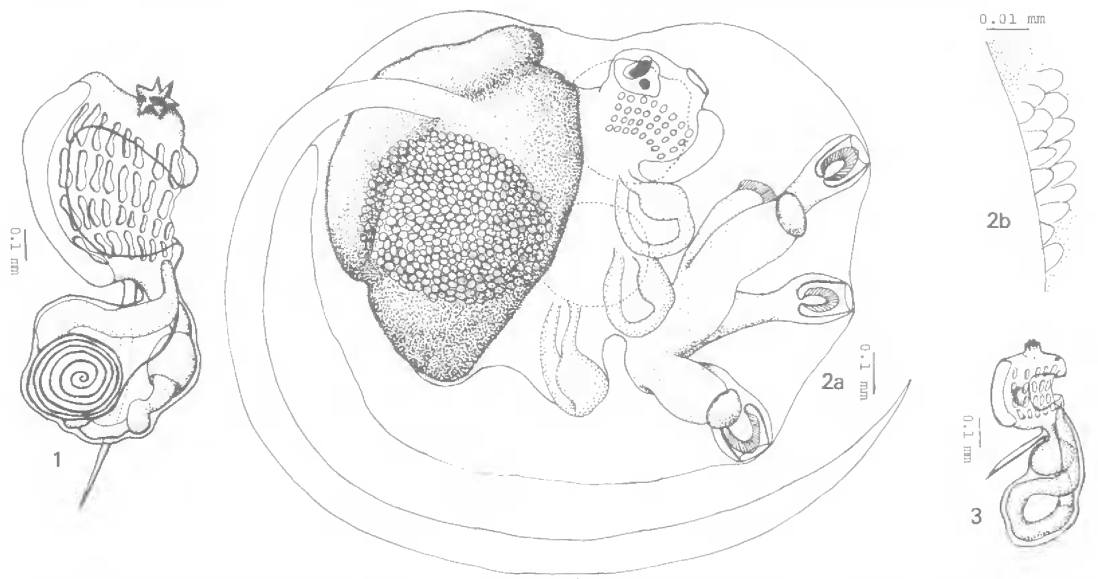
*Diplosomoides molle* Herdman, 1886, p. 310. Sluiter, 1909, p. 85; 1913, p. 78.

Not *Lissoclinum molle:* Kott, 1977, p. 618 (< *L. bistratum).* Newcomb and Pugh, 1975, p. 533 (< *L. punctatum*).

*Didemnum ternatanum:* Van Name, 1918, p. 152. Tokioka, 1955, p. 47; 1967, p. 77; 1975, p. 326. Kott, 1966, p. 287; 1977, p. 618. Vasseur, 1970, p. 213. Newcomb and Pugh, 1975, p. 533. Millar, 1975, p. 229.

Not *Didemnum ternatanum:* Kott, 1972, p. 179.

*Didemnum sycon* Michaelsen, 1920, p. 44.




FIGS. 1–2: *Didemnum molle* (QM G9780) — 1, zooid; 2, larva (a, from right side; b, ectodermal scales on posterior haemocoelic chamber).

FIG. 3: *Didemnum viride* (BM 07.8.30.41) — zooid.

## Material Examined

NEW RECORDS: Heron I.: January 1976, LWM, QM G9953 (juveniles); March 1975, 18 m, QM G9438 (juveniles); July 1975, 5 m, QM G9439 (juveniles); October 1976, LWM QM G9794 (juveniles); October 1979, LWM QM G12629 (juveniles); December 1976, 9 m, QM G11900 (mature gonads, larvae). Lewellyn Reef: August 1975, 3–9 m, QM G9765 (mature ♂). Lizard I.: June 1976, on coral rock shallow water, LWM, QM G9914 and G9979 (juveniles), QM G9777 (mature gonads some embryos), QM G9778 (larvae); on artificial reef 3–4 m between Lizard I., Palfrey I. and Solomon I., QM G9780 (mature gonads and larvae). Palau Is., 1979, LWM, QM G12680-2.

PREVIOUSLY RECORDED: *Diplosomoides molle* Herdman, 1886, Holotype BM 87.2.4.446. *Didemnum sycon* Michaelson, 1920, Types ZMH K1088, 1089; Van Name det., USNM 7384 (Philippine Expedition). *Didemnum molle* > *D. ternatanum:* Van Name, 1918, AMNH Chordata 2138, 2139, 2140. *Didemnum ternatanum,* Van Name det., USNM 5982, 2988 (Albatross), 6339; Tokioka, 1967, USNM 11404; Kott, 1977, QM G9652 (juveniles).

## Distribution

RANGE: Malagasy, Zanzibar (Michaelsen 1920, Vasseur 1970). Western Australia: Cockburn Sound (Kott 1977). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I. to Heron I. (Kott 1977). Indonesia (Sluiter 1909). Aru I. (Herdman 1886). Palau I. (Tokioka 1955, 1967). Philippines (Van Name 1918, Tokioka 1967, Millar 1975). Okinawa (Tokioka 1975).

HABITAT: Specimens have been taken from intertidal to 69 m (Sluiter 1909). Van Name (1918) reported the species growing on coral, shells, eel grass and other ascidians in shallow water. However, most of the stations from which specimens were reported by that author were in waters of 16–40 m, and only a few stations may have been in shallower water. Sluiter (1909) recorded specimens from reefs (intertidal?) to 69 m. In the present collection, the most robust colonies are in fairly protected habitats (in caves, under ledges, and in lagoons) in waters of 2–10 m, usually on dead coral, or rocky substrates. Smaller more or less flat colonies present under boulders near the reef crest, appear only to be juvenile colonies, and seldom achieve the typical hemispherical or stalked facies, although some have been found in pools near the LWM at Lizard I. These soft, flaccid colonies that secrete massive amounts of mucus when disturbed, do not appear to be adapted to intertidal habitats, or habitats on other than firm surfaces.

## Description

COLONY: The colonies are characteristically dome- to flask-shaped, with a common cloacal aperture in the centre of the upper surface. Some reach a diameter of 10 cm. They are firmly attached to the substrate by fine strands of spicule-filled test. The surface is smooth with a thin layer of very small spicules (0.005 to 0.015 mm) in the surface test. The spicules, together with a variable amount of brown pigment (especially dense in the vicinity of the common cloacal aperture) affect the colour of the colonies which may be from grey to reddish brown. Spicules are absent from the surface test between zooid openings only in very immature colonies when the green colour of the symbiotic algae is clearly visible. The 6 branchial lobes are conspicuous on the surface, each covered with corresponding lobes of spicule-filled test. One of the most conspicuous characteristics of this species is the soft and easily torn test, and the excessive amounts of mucus that are secreted by the living colonies. The common cloacal cavity is extensive, occupying most of the centre of the colony, and is lined with symbiotic algal cells. Zooids are contained in the soft test strands that cross the cloacal space, connecting the surface to the basal test, or to the core of test that projects from the base up into the centre of the colony.

Juvenile colonies are small, flat and predominantly green, the small spicules being present only around the apertures. In preservative the juveniles are an almost completely transparent reddish brown colour.

ZOOIDS: Zooids are up to 1·5 mm long. The thorax is especially long with 8–10 elongate rectangular stigmata. The wide atrial opening exposes most of the branchial sac. The 6 branchial lobes are pointed and their position where they open onto the surface is clearly marked by the spicules that are contained in the test. There is a long slender retractor muscle. The gut loop posterior to the stomach is curved ventrally. The vas deferens coils 6·5 times around the rather flat ♂ follicle.

LARVAE: These incubate in the central or basal test, the embryo having moved down the test connective in which the zooid is embedded. They are never present in the transparent juvenile colonies, found near the low water mark. The occurrence of these juvenile colonies suggests that breeding occurs throughout the year. Mature

colonies with ripe gonads and sometimes with embryos taken in June, August and December, support this hypothesis.

The larvae are about 0·9 mm long, excluding the tail, which is long and wound three quarters of the way around the larval trunk. There is an oozooid, with ocellus and otolith, and two blastozooids. Anteriorly a more or less rectangular frontal plate, supports the short rather thick stalks of the 3 median adhesive organs. The adhesive cells are arranged in a long rather narrow cone, surrounded by a deep ectodermal cup. As the larva matures, the frontal plate extends forwards on a rather narrow stalk and four long cylindrical ectodermal ampullae are produced from each corner of the frontal plate. There are modified columnar cells on the rounded ends of the ectodermal ampullae. The posterior haemocoelic chamber (erroneously referred to by Kott, 1977, as a 'pouch') into which the tail is inserted, is large and slightly flattened antero-posteriorly. The vacuolated cells referred to by Millar (1975) appear to be yolk cells from the spherical mass of yolk behind the blastozooids. These cells gradually disperse and some are found in the haemocoelic chamber. When the tail is extended the haemocoelic chamber becomes almost spherical and the plant cells adhere to the larval test outside it. A few larvae have been found with the larval tail prematurely withdrawn into this chamber while they are still in the common cloacal cavity of the adult colony (Kott 1977). In the mature larva there are flattened, overlapping scales on the ectoderm of the haemocoelic cavity. Their function is not known, but they resemble ectodermal cells of the rastrum or plant rake in *Diplosoma* spp. and possibly they are associated with the adhesion of the plant cells that cover the test in this region. The two abdominal buds are on the right side of the larva and the thoracic buds are on the left.

REMARKS: The colonies, their spicules, and the copious quantities of mucus that are produced are quite distinctive and the species is readily recognised. The atrial opening that exposes most of the branchial sac, so that the peribranchial cavity is almost entirely lost, is reminiscent of the condition in *Lissoclinum patellum* and *Diplosoma* spp. The larval blastozooids are also reminiscent of the larva of *Lissoclinum bistratum,* as are the modified columnar cells on the ectodermal ampullae. The deep, narrow ectodermal cups and elongate cone of the adhesive organs are unique features of the larva.

Van Name (1918) erroneously identified specimens of this very characteristic species as *D. ternatanum,* and illustrated his description liberally. Subsequent authors accepted Van Name's identification and so perpetuated his mistake. Examination of his specimens, and of the types of *D. molle* and *D. sycon* has established their true identity. Van Name himself was aware of his error, and corrected the labels of these specimens in the American Museum of Natural History.

Colonies have been observed to move up sides of aquaria at 1·5 cm per day over a period of at least 7 days (D. Griffiths, pers. comm.). Movement may be in response to subminimal conditions by successive growth and resorption of adhesive test strands as in *Diplosoma listerianum* (Carlisle 1961). It may cause clustering of colonies observed at the top of *Acropora* debris in lagoons.

**Didemnum viride** (Herdman, 1906)
(Fig. 3; Plate 1·2)

*Leptoclinum viride* Herdman, 1906, p. 34.
*Didemnum viride* Vasseur, 1970, p. 216.
Not *Tridemnum viride:* Tokioka, 1967, p. 87 (< *Tridemnum* spp.).

MATERIAL EXAMINED

NEW RECORDS: None.

PREVIOUSLY RECORDED: *Leptoclinum viride* Herdman, 1906. Holotype, BM 07.8.30.41.

DISTRIBUTION

RANGE: Ceylon (Herdman 1906). Malagasy (Vasseur 1970).

HABITAT: The holotype is from 2·5 m, south of Periya Paar, Ceylon. It is investing a skeletal fragment of *Campanularia juncea* (*fide* Herdman 1906). The specimen from Malagasy is from a blade of sea grass.

DESCRIPTION

COLONY: The colony is an extensive encrusting sheet, about 3 mm thick. The surface is marked into rounded and slightly raised areas by slight depressions over the common cloacal canals. The zooids are arranged along either side of these canals. The branchial apertures are evident on the surface of the colony as minute prominences. In the preserved specimen there is a very thin superficial layer of bladder cells mixed with algal cells. The remainder of the test is crowded with the conspicuously stellate calcareous spicules 0·03–0·04 mm in diameter. The thoraces of the zooids are firmly embedded in the test along their ventral surface. The cloacal canal is fairly restricted and is at thoracic level.

ZOOIDS: These are very small, about 0·7 mm. The branchial aperture is 6–lobed and the atrial opening is wide. There is a large oval lateral organ in the middle of each side of the thorax. There are four rows of only five oval stigmata. The three languets of the dorsal lamina are especially long. There are the usual very fine muscle fibres on the thorax that extend from between the rows of stigmata into two bands in the pharyngeal wall either side of the dorsal lamina and into the short retractor muscle where they are joined by fibres from the outer wall of the atrial cavity.

The abdomina are firmly embedded in the solid basal test. There is a narrow duodenal area. The intestine curves ventrally and to the left before curving dorsally and then anteriorly so that the part of the gut loop distal to the stomach bends ventrally at an angle to the long axis of the zooid. There is conspicuous glandular material in the loop of the gut. The zooids in the colony are not sexually mature.

REMARKS: Owing to the lack of gonads in both recorded specimens, the generic status of this species is unconfirmed. However the oval stigmata, the flat lateral organ and the secondary curve of the gut loop suggest that *Didemnum,* rather than *Lissoclinum,* is the appropriate genus. The small size of the zooid, conspicuously stellate spicules and flat oval lateral organ together with embedded plant cells distinguish this species from other algal containing didemnid species that are presently known.

**Tridemnum clinides** Kott, 1977
(Figs. 4, 5; Plates 3·1a,b)

*Tridemnum clinides* Kott, 1977, p. 617.
*Tridemnum viride:* Tokioka, 1967, p. 87 (part, zooids with atrial siphons).
*Tridemnum* sp. Eldredge, 1967, p. 184.

MATERIAL EXAMINED

NEW RECORDS: Viti Levu, Fiji, August 1979: Votualailai, under cascades, fringing reef, QM G12620.

PREVIOUSLY RECORDED: *Tridemnum clinides* Kott, 1977, Holotype QM G9928 (with larvae); Paratypes QM G9931. *Tridemnum viride:* Tokioka, 1967, USNM 11646.

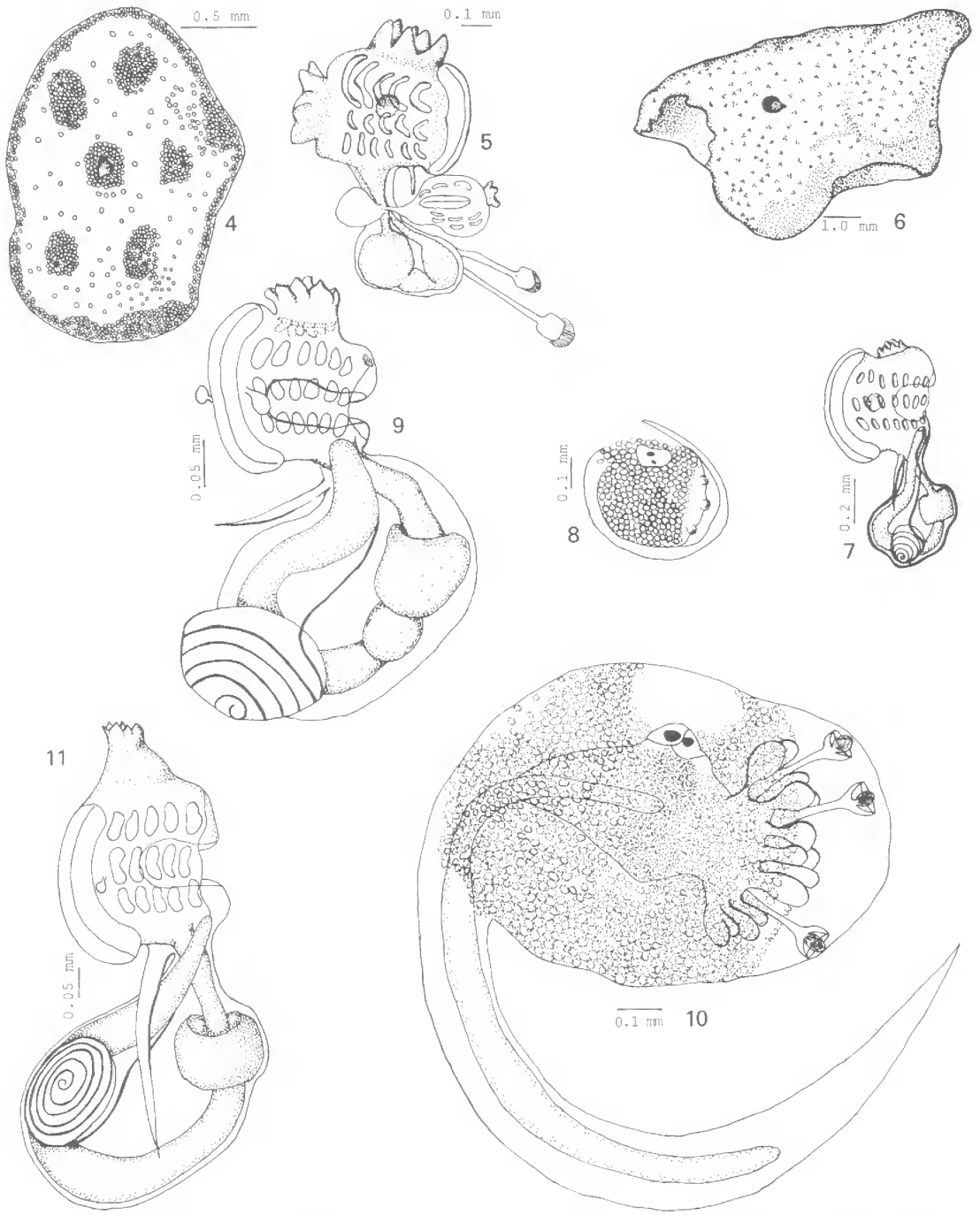
DISTRIBUTION

RANGE: Great Barrier Reef: Heron I. (Kott 1977). Fiji: Votualailai (new record). Philippines (Tokioka 1967). Eniwetok (Eldredge 1967).

HABITAT: At Heron I. the species occurs just below the low tide mark in cryptic habitats near the reef edge and in the lagoon (where it is more common). The Fijian specimens were taken where the water of the fringing reef flat drains into the river channel that bisects it. The colonies are found deep in the dense algal mat that covers the reef beneath these cascades, where a fast unidirectional current flows for about half of each tidal cycle. The Philippine specimens were also taken from shallow water but little other information is available concerning their habitat.

DESCRIPTION

COLONY: The colonies are small, almost spherical or oval or slightly irregular. Large colonies are more or less flattened on the upper surface. The zooids are arranged in a single circle toward the periphery of the colony, and there is a single central common cloacal opening in the centre of the upper surface. The test is very soft. The basal test and sometimes extensions of it attach the colonies to the substrate and they are often difficult to remove. There is a thin superficial layer of bladder cells. Spicules are sometimes but not always, dense in the border and base of the colonies. They are quite sparse in the surface of the colony except where there are dense patches over the anterior end of each zooid. The branchial apertures actually open toward the outer border of each of these patches of spicules. Elsewhere the spicules are evenly distributed and mixed with the algal cells that are embedded throughout the soft test. Algal cells are most




FIGS. 4–5: *Tridemnum clinides* (QM G12620) — 4, colony from the upper surface showing distribution of spicules, and branchial and cloacal apertures; 5, zooid with buds and stolonic vesicles (gonads not shown).

FIGS. 6–8: *Tridemnum miniatum* (QM G12478) — 6, colony; 7, zooid; 8, larva.

FIGS. 9–10: *Tridemnum strigosum* (USNM 11681) — 9, zooid; 10, larva.

FIG. 11: *Tridemnum nubilum* (USNM 11641) — zooid.

common in the surface test. The colonies are a pale cloudy mustard green owing to the mixture of spicules and plant cells throughout the test. The common cloacal cavity is thoracic, but rather deep, extending the whole length of the thorax. There are small accumulations of spicules where the atrial openings enter the cloacal cavity. There do not appear to be any plant cells lying free in the common cloacal cavity. Spicules are stellate, from 0·03 to 0·04 mm with a variable number of rounded or conical rays.

ZOOIDS: These are small (about 1 mm). The branchial lobes are deeply incised and there is a conspicuous short, wide atrial siphon with its border produced into six shallow obtuse lobes. There are 3 rows of 5 long rectangular stigmata in each of the 3 rows. There is a rounded lateral organ in the centre of the thorax and a very short retractor muscle. The gut loop is of the usual form with the vas deferens wound 6·5 times around the ♂ follicle. The zooids are colourless but there is often some brown pigment in the test.

LARVAE: These have been taken from specimens collected at Heron I. in January (QM G9922) and in the Philippines in January. They were not present at Votualailai in July. They are 0·6 mm long and the mature larva is enveloped in a dense coat of plant cells that are absent only from areas around the anterior end of the larva to expose the 3 median adhesive papillae, and a circular area over the otolith and ocellus. Ectodermal ampullae are characteristically short and rounded, at either side of the base of the stalks of the adhesive organs.

REMARKS: Tokioka (1967) believed *Didemnum viride* (Herdman, 1906) to be synonymous with a species of the genus *Trididemnum* which has been found to include specimens of the present species. All the species have plant cells embedded in the superficial layer of test. However, the 4 rows of stigmata that is characteristic of the genus *Didemnum* has been confirmed for Herdman's species. *Trididemnum viride:* Tokioka, 1967, includes specimens of *T. miniatum* and two new species of *Trididemnum* in addition to the present species. The possible habitat preferences of *T. miniatum* and the present species are discussed below.

The atrial siphon also distinguishes the present species from *T. cyclops* (which has similar spicules). They are further distinguished by the distribution of spicules, which in *T. cyclops* appear from the surface to be in a dense concentration around each branchial siphon that is continuous with the concentration of spicules around the border of the colony.

*Didemnopsis globuliferum* Sluiter, 1913, which Tokioka (1967) has suggested as synonymous with his specimens, appears to be a junior synonym of *Trididemnum discrepans* (Sluiter, 1909).

### **Trididemnum miniatum** Kott, 1977
(Figs. 6–8; Plate 3·2)

*Trididemnum miniatum* Kott, 1977, p. 617.
*Trididemnum viride:* Tokioka, 1967, p. 8 (part, colonies with smaller spicules).

MATERIAL EXAMINED

NEW RECORDS: Green I.: August, 1979, on seagrass, south of jetty, close inshore (with larvae), QM G12478. Heron I.: October 1979, cryptic near reef edge below LWM (with larvae) QM G12622.

PREVIOUSLY RECORDED: *Trididemnum miniatum* Kott, 1977, Syntypes QM G9927 (with larvae); Paratypes QM G9945. *Trididemnum viride:* Tokioka, 1967, USNM 11661 (part), USNM 11796 (part).

DISTRIBUTION

RANGE: Great Barrier Reef: Heron I. (Kott 1977); Green I. (new record); Philippines (Tokioka 1967).

HABITAT: The species has been taken with *T. cyclops* on coral debris and on weed below the low tide mark in cryptic habitats behind the reef crest and in the lagoon at Heron I. At Green I. however, the species was taken on the sandy inner reef flat, attached to sea grass blades. Philippine specimens are also taken in very shallow water.

DESCRIPTION

COLONY: These are small and rounded to elongate. Some colonies are up to 1·0 cm in their maximum dimension, but more often they are about 4 mm in diameter. They are white to lime green or emerald green depending on the concentration of spicules in the test where they are mixed with algal cells. There are some fine veins of red pigment in the surface test in fresh material. Spicules are either present or absent in the superficial layer of test where the algal cells are most dense, and are quite dense throughout the remainder of the test, providing a white background for the green cells in the surface

layers of the colony that emphasises their colour. Spicules are usually absent from the surface test in the areas just over the zooids, although they are often present in the tips of the branchial lobes. The algal cells become progressively less dense toward the base of the colony where they are absent altogether. They are also present in the common cloacal canal. The spicules are only 0·01 to 0·02 mm, spherical, with numerous blunt ended rays. There is no conspicuous superficial layer of bladder cells in this species. The common cloacal canal is shallow and thoracic. The colonies are attached only lightly to the substrate by strands of test and are easily removed.

ZOOIDS: These are about 0·8 mm long. They are orange in fresh material but become colourless in preservative. The 6 branchial lobes are sharply pointed. The atrial opening is wide and transverse exposing most of the middle portion of the branchial sac. There is a rounded lateral organ half way down the branchial sac. There are 7 longish oval stigmata in each of the three rows. There is a fairly long retractor muscle from the posterior end of the thorax, extending most of the length of the abdomen. The gut loop is of the usual form, and the vas deferens coils 5·5 times around the ♂ follicle.

LARVAE: Larvae are present in most of the colonies that have been collected. They are known to be present from August to January. It is possible that this small and inconspicuous species breeds throughout the year. Mature ♂ gonads were present in the Green I. colonies but not in those from Heron I. in either October or December and it is probable that testes mature before the ovary. The larvae are of the usual *Tridemnum* form with a coat of algal cells present in the mature specimens. This algal coat is interrupted over the otolith and ocellus, and at the anterior end of the larval trunk, exposing the adhesive organs. There are 3 adhesive organs in the median line and 3 pairs of elongate ectodermal ampullae. The larval trunk is 0·7 mm long.

REMARKS: The relatively small spherical spicules and their absence from the test immediately over the anterior end of the zooids helps distinguish this species from two others from the Philippines with which Tokioka (1968) had confused it. All three species have small zooids and algal cells embedded in the test and all lack the atrial siphon of *T. clinides*. The present species often shares a habitat with *T. clinides*. Although both have a wide geographic range that includes the Philippines and the Great Barrier Reef, *T. miniatum* was not taken with *T. clinides* at Votualailai, nor was *T. clinides* taken with *T. miniatum* at Green I. Thus, they may have slightly different ecological requirements, the softer more delicate *T. clinides* possibly being less tolerant of reef flat conditions than the smaller *T. miniatum,* which however, makes a less robust attachment to the substrate than *T. clinides,* and is less often found where strong water flow and turbulence is likely to affect it. Further to the south (at Heron I.) *T. miniatum* is found in the lagoon and near the edge of the reef in cryptic habitats, but not on the sandy inner reef flat where it is found at Green I.

### **Tridemnum strigosum** n. sp.
(Figs. 9, 10; Plate 3·3)

*Tridemnum viride:* Tokioka, 1967, p. 87 (part, spicules with fewer rays).

MATERIAL EXAMINED

PREVIOUSLY RECORDED: *Tridemnum viride:* Tokioka, 1967, Holotype and Paratypes USNM 11681 (part, with larvae), 11640 (part), 11641 (part), 11642, 11649, 11661 (part), 11672 (part), 11796 (part).

DISTRIBUTION

RANGE: Philippine Is (Tokioka, 1967).

HABITAT: The species has been taken principally on algae and sea grass at depths of 1–6 m.

DESCRIPTION

COLONY: Colonies are very thin investing sheets up to 2 cm in length. They are closely applied to the surface of the substrate, investing weed and sometimes coral fragments, and are consequently very irregular. Sometimes the colonies are elongate and lobulating. The test is densely packed with large stellate spicules, 0·05–0·08 mm in diameter, with 7 conical pointed rays in optical section. The test is brittle and its surface is granular owing to the density of the spicules contained in it. Plant cells are found embedded in the superficial layer of test above the spicules. They are especially small (0·004–0·01 mm). The cloacal cavity is thoracic and very limited. Zooids are evenly spaced, about 1 mm apart, and are seen from the surface as dark points interrupting the spicules.

ZOOIDS: Zooids are extremely small, only about 0·5 mm in total length. The dark pigmentation is usually conspicuous around the branchial aperture. There is a distinct branchial siphon with 6 triangular lobes. The atrial aperture is a transverse incision. There are 3 rows of 7 elongate-oval stigmata. A stalked lateral organ projects outwards from opposite the second row of stigmata on either side of the endostyle. The retractor muscle is of moderate length. The gut loop is fairly long, and flexed ventrally with a distinct right-angle bend in the rectum where it extends anteriorly. The ♂ follicle is deep and with 5·5 coils of the vas deferens.

LARVAE: Larvae are present in the colonies from Basilau I. in January. They lie in the test where they become surrounded by a capsule of plant cells that become embedded in the larval test. They are about 1·1 mm long with a short tail extending only half way around the larval trunk. There are 6 to 8 pairs of ectodermal ampullae that arise from the frontal area around the stalks of the three adhesive organs. The variation in the number of ectodermal ampullae is caused by their subdivision. The frontal area is separated from the central area of the larval trunk where the developing oozooid expands. The posterior haemocoelic chamber tapers posteriorly around the base of the tail. The plant cells embedded deep in the larval test are absent only from the area over the sense organs and anteriorly in front of the adhesive apparatus. As the oozooid swells in the centre of the larval trunk, the test and its contained plant cells becomes thinner in this area and the developing oozooid can be seen.

REMARKS: The zooid of the present species resembles that of *T. miniatum*, although it is even smaller. The species is distinguished by its very large and dense stellate spicules, and its large larva with embedded plant cells. The thin investing colonies are also characteristic.

### **Tridemnum nubilum** n. sp.
(Fig. 11; Plate 3·4)

*Tridemnum viride:* Tokioka, 1967, p. 87 (part, specimens with numerous rays).

MATERIAL EXAMINED

PREVIOUSLY RECORDED: *Tridemnum viride:* Tokioka, 1967, Holotype and Paratypes USNM 11641, 11640 (part), 11659 (part), 11661 (part), 11672 (part), 11680, 11681 (part), 11796 (part).

DISTRIBUTION

RANGE: Philippine Is. (Tokioka 1967).

HABITAT: The habitat is apparently the same as that of the previous species, and is found on weed, in shallow water, and on or in the vicinity of coral reefs.

DESCRIPTION

COLONY: The colonies are small and irregular but rather solid. The spicules are evenly spaced in the solid gelatinous test which is translucent and a slightly pink-brown colour in preservative. Spicules are seldom dense in any part of the test and sometimes they are sparse in the middle layers of test. The spicules are large (0·03–0·05 mm diameter). They are almost spherical, with about 10–14 short pointed rays in optical section. There are occasional spicules with blunt rays. The plant cells are slightly larger than those of *T. strigosum* (about 0·015 m diameter). They are mixed with the spicules in the upper layer of test, above the common cloacal cavity. It is this mixture of spicules, plant cells and test that confer the rather fluffy, soft appearance to the colony that is also reminiscent of *T. clinides*.

ZOOIDS: Zooids are evenly spaced in the colony and are sometimes brown in the preserved specimens. They are small, about 0·6 mm in total length. The branchial lobes are minute, the atrial aperture is a deep transverse incision and there is a conspicuous flat circular mass of spicules in the lateral organ which projects outwards on either side of the endostyle. There are three rows of 5 elongate-oval stigmata. The retractor muscle is strong and is sometimes very long. The gut forms a simple horizontal loop and the single ♂ follicle with 5·5 coils of the vas deferens, is rather flat in comparison with *T. strigosum*. Testes were mature in most of the colonies but no larvae were found.

REMARKS: This species with its incised atrial aperture, very small zooids and embedded plant cells, is distinguished from *T. miniatum* and *T. strigosum* by its large, almost spherical spicules, strong retractor muscle, and tough gelatinous test and translucent appearance. *T. clinides* resembles the present species in external appearance but is readily distinguished by its atrial aperture, larger zooids and smaller stellate spicules with fewer rays. The spicules resemble those of *T. paracyclops* but in the latter species zooids are larger and plant cells are confined to the common cloacal cavity.

**Tridemnum cyclops** Michaelsen, 1921
(Figs. 12–14; Plates 4·1 a,b)

*Tridemnum cyclops* Michaelsen, 1921, p. 19. Hastings, 1931, p. 89 Kott, 1962, p. 581; 1966, p. 286; 1977 (part), p. 616. Eldredge, 1967, p. 183. Tokioka, 1967, p. 85 (part). Thorne, Newcomb and Osmond, 1977, p. 575.

Not *T. cyclops* Newcomb and Pugh, 1975 p. 534 (< *Didemnum* sp.)

*Lissoclinum pulvinum:* Tokioka, 1967, p. 97 (part).

MATERIAL EXAMINED

NEW RECORDS: Fiji (Viti Levu) fringing reefs, July 1979: Vuda Point, in pools below the low water mark, outer reef flat, QM G12453 (some larvae); Tailevu, amongst living coral at low water mark on reef edge, QM G12455; Makaluva reef, in pools at low water outer reef flat, QM G12460. Fiji (Viti Levu), fringing reefs, August 1979: Votualailai, beneath cascades tangled in algal mat, QM G12619.

PREVIOUSLY RECORDED: *Tridemnum cyclops* Michaelsen, 1921, Syntypes, ZMH K1110; Tokioka, 1967, USNM 11482, 11483; Kott, 1977, QM G9942 (with larvae), G9944. *T. viride:* Tokioka, 1967, USNM 11661 (part). *Lissoclinum pulvinum* Tokioka, 1967, USNM 11480 (part), 11643 (part), 11684 (part), 11669 (part).

DISTRIBUTION

RANGE: Malagasy (Michaelsen 1921). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I. to Heron I. (Hastings 1931, Kott 1977). Philippines (Tokioka 1967). Gilbert I. (Tokioka 1967). Fiji: Viti Levu (new record). Eniwetok (Eldredge 1967).

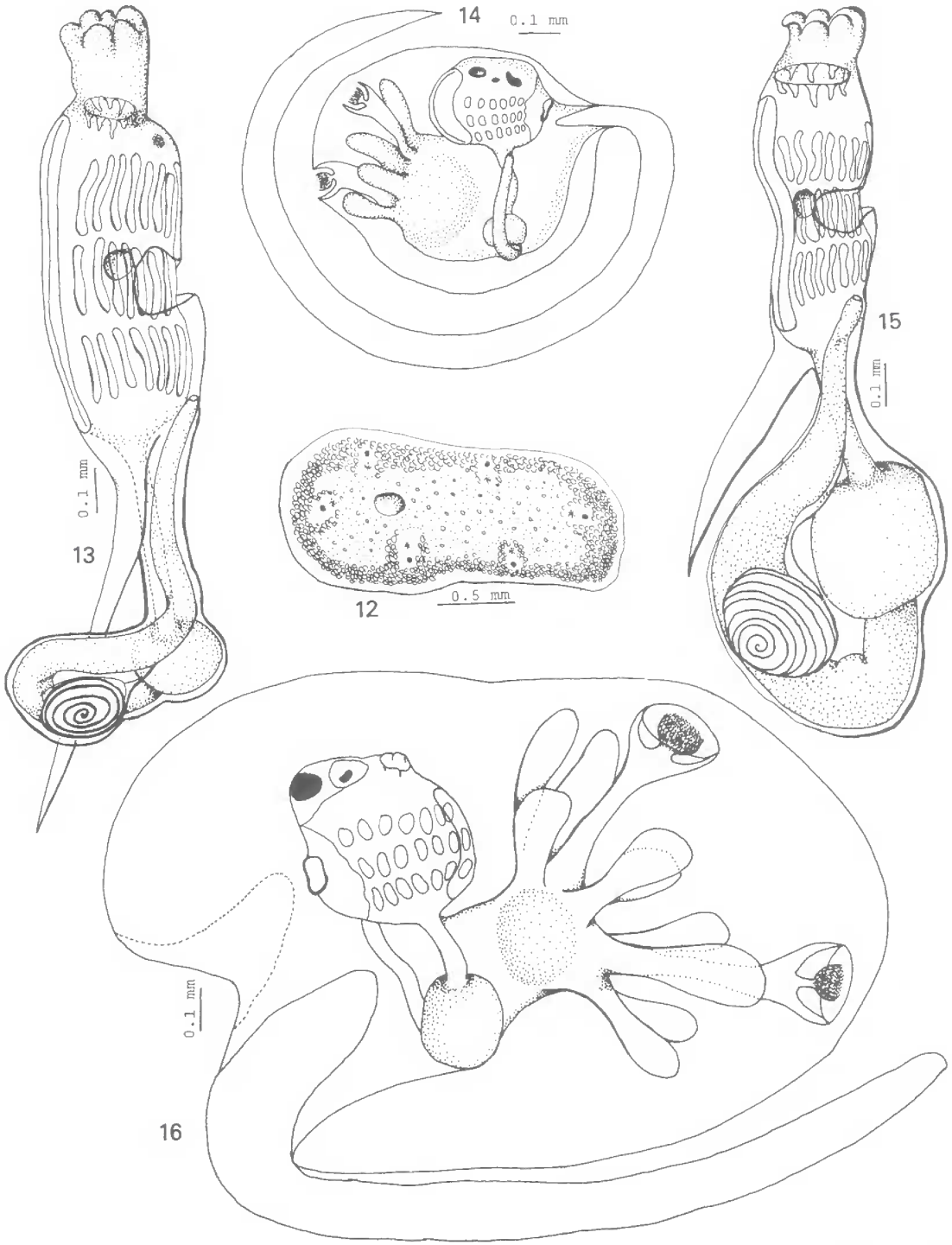
HABITAT: The species lives in cryptic habitats on weed, coral and rocks just below the low water mark in pools behind the reef crest and in the lagoon, and between coral branches and in the interstices of algal mats at the reef edge. It is a common species but is found generally where water flow is not strong, or in habitats where it is well protected, and usually where it is well shaded. It is often found with *Lissoclinum bistratum* and *T. miniatum*. With *Tridemnum miniatum* and *Diplosoma virens* it is found in deeper and less exposed locations at Heron I. than at locations further to the north.

DESCRIPTION

COLONY: These are characteristically small and oval, usually less than 1 cm in length. Dense spicules line the borders and base and there is a thick superficial layer of bladder cells that surround the colony, usually extending around onto the base. This bladder cell layer is less dense on the upper surface. The spicules are usually absent from the upper surface, which is green owing to the plant cells in the thoracic common cloacal cavity. There is usually a single system in each colony, with a central, sessile cloacal aperture. Colonies appear to divide when they exceed 0·5 cm in length. A constriction in the border eventually spreads across the surface and divides the colony from the surface toward the base (see specimens QM G12453, Vuda Point, Viti Levu, July, 1979). The zooids are arranged around the border, their ventral surface embedded in the test. The presence of the zooids around the circumference of the colony creates their characteristic surface appearance. Each whitish zooid projects into the green algal-filled cloacal cavity from the white spicule-filled border of the colony. The dark endostylar pigment cap is visible on the anterior surface of each of the zooids. There may be a single layer of spicules, of varying concentrations over the remainder of the surface test beneath the bladder cell layer. The spicules are fairly dense in a layer beneath the shallow thoracic common cloacal cavity but become less dense toward the base of the colony. There are 0·03–0·04 mm in diameter with some at 0·06 mm. There are two types of spicules, the most numerous with about 12–14 conical pointed rays in optical cross section. There are also spicules with more numerous, almost parallel sided rays.

ZOOIDS: These are almost 1·5 mm long when extended. The branchial aperture has 6 pointed, deeply divided triangular lobes. The atrial aperture is a deeply incut opening. There are 7 long oval stigmata in each of the three rows. The retractor muscle is long and broad where it arises from the neck of the zooid. The abdomina are embedded in basal test and are only about one quarter of the length of the thorax. The gut loop is flexed ventrally. The vas deferens coils 5·5 times in an anti-clockwise direction around the ♂ follicle.

LARVAE: Although they are present in colonies from Viti Levu in July, the more prolific colonies were those from Heron I. lagoon in December 1976 (QM G9942), and from Keeper Reef off Townsville in August 1977. In some colonies mature eggs and larvae are present but ♂ glands appear to be spent suggesting their earlier maturation. The species may breed throughout the year, with a peak in larval production in the summer months. Mature embryos are 0·5 mm long. They begin their development in the basal




FIGS. 12–14: *Trididemnum cyclops* (QM G9942) — 12, colony showing endostylar pigment caps and distribution of spicules beneath the superficial bladder cell layer; 13, zooid; 14, larva.

FIGS. 15–16: *Trididemnum paracyclops* (QM G12628) — 15, zooid; 16, larva.

test and subsequently move into the common cloacal cavity where they acquire a coating of plant cells that is interrupted over the sense cells and around the front of the larval body to expose the two adhesive organs. The tail is stout and is wound three quarters of the way around the larval trunk. There are two pairs of ectodermal ampullae and the characteristic two adhesive organs.

REMARKS: The species is distinguished by the size of the colonies, by the single systems in which zooid are restricted to the border of the colony. The solid translucent superfical layer of bladder cells and the endostylar pigment cap occur in a related species of this genus (see below) which is distinguished by the size of the colony, a relatively large abdomen and greater number of vas deferens coils and the size of the larva and the number and modification of its ectodermal ampullae.

**Tridemnum paracyclops** n. sp.
(Figs. 15, 16; Plates 4·2 a,b)

*Tridemnum spiculatum* Kott, 1962, p. 281 (part, specimen from Heron I.).
*Tridemnum cyclops:* Kott, 1977, p. 47 (part, extensive sheets).

MATERIAL EXAMINED

NEW RECORDS: Heron I.: October 1979, cryptic habitats in pools behind reef crest, Holotype QM G12627, Paratypes QM G12628 (with larvae).

PREVIOUSLY RECORDED: *Tridemnum cyclops:* Kott, 1977, QM G9446, G9788, G9909, G9910, G9912, G9915, G9916, G9917, G9918, G9940, G9941 (with larvae), G9943 (with larvae), G12630 (with larvae). *Tridemnum spiculatum* Kott, 1962 (part, specimen from Heron I.), AM Y1627.

DISTRIBUTION

RANGE: Great Barrier Reef (Lizard I. to Heron I.). It has been recorded principally from Heron I. where it appears to be very common but is also present amongst the specimens previously identified as *T. cyclops* (Kott 1977) from Lizard I. (QM G9912), Nymph I. (QM G9788), Wilson I. (QM G9940) and Northwest I. (QM G9917).

HABITAT: The species is found investing dead coral (*Acropora*) branches and rock in shaded cryptic habitats below the LWM, in deeper pools behind the reef crest.

DESCRIPTION

COLONY: Extensive and irregular investing sheets, up to 5 cm in greatest dimension and 2·3 mm thick. In one colony (QM G9943) a strip of the colony has overgrown the surface and fused with another part of the colony. This is a simple example of the phenomenon which, in *Tridemnum cerebriforme,* creates a most complex pattern. There is a superficial layer of bladder cells which surround the colony, extending around the border and onto its lower surface. In the border of the colony the spicules are fairly dense beneath this bladder cell layer. They are of variable, though even, density in the upper surface. The green colour of the colony is a result of the green plant cells seen through the surface test and it varies with the density of the white spicules in the surface layer of test. There is a dense layer of spicules below the shallow thoracic cloacal cavity (in which the algal cells occur) and beneath this they are absent altogether except for a single layer which is sometimes present where the test is attached to the substrate. Dark pigment occurs in the basal layer of test and sometimes in the zooids and this pigment often stains the preserving fluid most conspicuously. The spicules are large, from 0·03 mm to almost 0·08 mm. They are all of the one type with about 14 conical rays in optical transverse section.

Zooids are evenly and quite densely distributed in the colony. Sometimes the peripheral zooids are embedded in the test of the border of the colony, as in *T. cyclops,* but more often the cloacal cavity extends around between the border and the zooids, which appear, from the surface, to be surrounded by a thin layer of spicules (contained in the thoracic test sheath) and the green cells within the cloacal cavity. The zooids can be observed through the surface test, although they are not as conspicuous as in *T. cyclops.* Small colonies differ from *T. cyclops* in the large number of zooids which are crowded evenly in the colony and not just arranged around the periphery and the endostylar pigment cap is not always visible from the surface in the present species.

ZOOIDS: These are about 1·5 mm long when fully extended. The branchial lobes are fairly shallow. The atrial aperture is deeply incised. There are 7 stigmata in each of the three rows. The retractor muscle is relatively short and broad and does not extend beyond the abdomen. The abdomen is almost the same size as the thorax. The gut loop is fairly straight and is not flexed ventrally. There is a very large ♂ follicle with the vas deferens wound anti-clockwise 9·5 times around it.

LARVAE: Although most of the specimens collected are fairly robust, larvae are only present in small numbers in colonies collected in October

and December. They are not present in colonies taken in August, September, January and March at Heron Island, nor in the Nymph I. specimens in June. Mature ♂ follicles are present in colonies collected in October. The available data suggest a restricted breeding period in early summer (October to December). The larvae are exceptionally large, with a body 1 mm long, the tail wound only half way around. There are only two adhesive organs but there are four pairs of ectodermal ampullae and an additional unpaired dorsal one. The plant cells do not form a coat around the larva as in other species in this genus but are attached to an area at the posterior end of the body where the posterior haemocoelic chamber is extended around the base of the tail. The algal cells adhere to the larval test either side of the mid line. As the tail straightens, its proximal end, in the posterior haemocoelic chamber, is drawn down and a pocket develops just above it in the postero dorsal part of the larval test. The plant cells that adhere to this part of the larval test are accordingly enclosed in an incipient cloacal cavity that, in due course, receives the atrial openings of the zooids that surround it. The larvae are apparently free swimming for a very limited period and a larva has been observed in which the tail is in the process of resorption in the posterior haemocoelic chamber before the larva is released from the cloacal cavity. A round yolk mass persists until a late stage in the elongate frontal section of the larva.

REMARKS: The species was formerly thought to represent large colonies of *T. cyclops*. The larvae are almost twice the size of those of *T. cyclops*, they have more ectodermal ampullae, and the plant cells are differently distributed on them. Closer examination of both species has demonstrated differences in the colony, the spicules, the proportions of the zooids and their retractor muscles, the course of the gut, and the number of vas deferens coils.

It is also possible that colonies of *T. cyclops* lobulate when they reach a certain size while in *T. paracyclops* neither the size of the colony nor the number of zooids and systems in it are restricted in this way. The species is distinguished from *T. natalense* and *T. savignyii* by the absence of an atrial siphon and the presence of only two larval adhesive organs.

**Lissoclinum voeltzkowi** (Michaelsen, 1920)
(Figs. 17–19; Plates 1·3a,b and 1·4)

*Didemnum voeltzkowi* Michaelsen, 1920, p. 54. Hastings, 1931, p. 97.

MATERIAL EXAMINED

NEW RECORDS: Heron I.: March 1975, under rocks, rubble zone, near eastern end of south reef, QM G12633; December 1976, under rocks, rubble zone, eastern end of south reef; QM G12632. Green I.: August 1979, inner sandy reef flat, on brown algae, QM G12474 (with larvae). Lizard I.: June 1976, blue lagoon, on coral in shallow water, low tide, QM G9913, G12621 (with larvae). Fiji (Viti Levu) July 1978: Malevu, fringing reef, sandy reef flat, QM G12479 (with larvae); Suva Barrier Reef, sandy reef flat, G12472 (with larvae); Makaluva reef, sandy reef flat, G12473 (with larvae). Fiji (Viti Levu) August 1979: Votualailai under cascades in interstices of algal mat QM G12617. Philippines: Van Name *det.* AMNH Chordata 2128.

PREVIOUSLY RECORDED: *Didemnum voeltzkowi* Michaelsen, 1920, Types ZMH K1099, K1111; Hastings, 1931, BM 30.12.17.44 (one colony in the Australian Museum, Sydney), BM 30.12.17.43.

DISTRIBUTION

RANGE: Malagasy (Michaelsen 1920). Great Barrier Reef: Low Is. (Hastings 1931); Green I. and Heron I. (new records). Fiji: Viti Levu (new records). Philippines (new record).

HABITAT: The habitat requirements of this species are possibly the most restricted of all the plant-bearing didemnid species (with the exception only of the endemic diplosomid from Viti Levu). They are found near the low tide mark, on the outer part of the open sandy reef flat. They are not normally cryptic. They often occur on weed (including *Halimeda*). On the fringing reefs of the Fijian island of Viti Levu a mosaic of colonies of this species, each colony contiguous along its borders with adjacent colonies, covers vast areas of the sandy reef flat inshore from the living coral zone. They were absent only from the northern fringing reefs at Tai Levu. On the Great Barrier Reef at Green I. the species is also found in abundance inshore from the living coral zone of the reef flat although at this location it is attached to sea-weed and is not lying on the sandy sediments. At Heron I. the relatively small number of small colonies are from the rubble zone near the reef edge at the eastern end of the reef, and at one location on the southern edge of the reef.

DESCRIPTION

COLONY: The living colonies are a dirty greyish brown or cream or greenish cream with dense brown-black pigment contained in spherical cells that are scattered in the surface test and also gathered into small evenly spaced patches between the zooids around the edge of the colony and

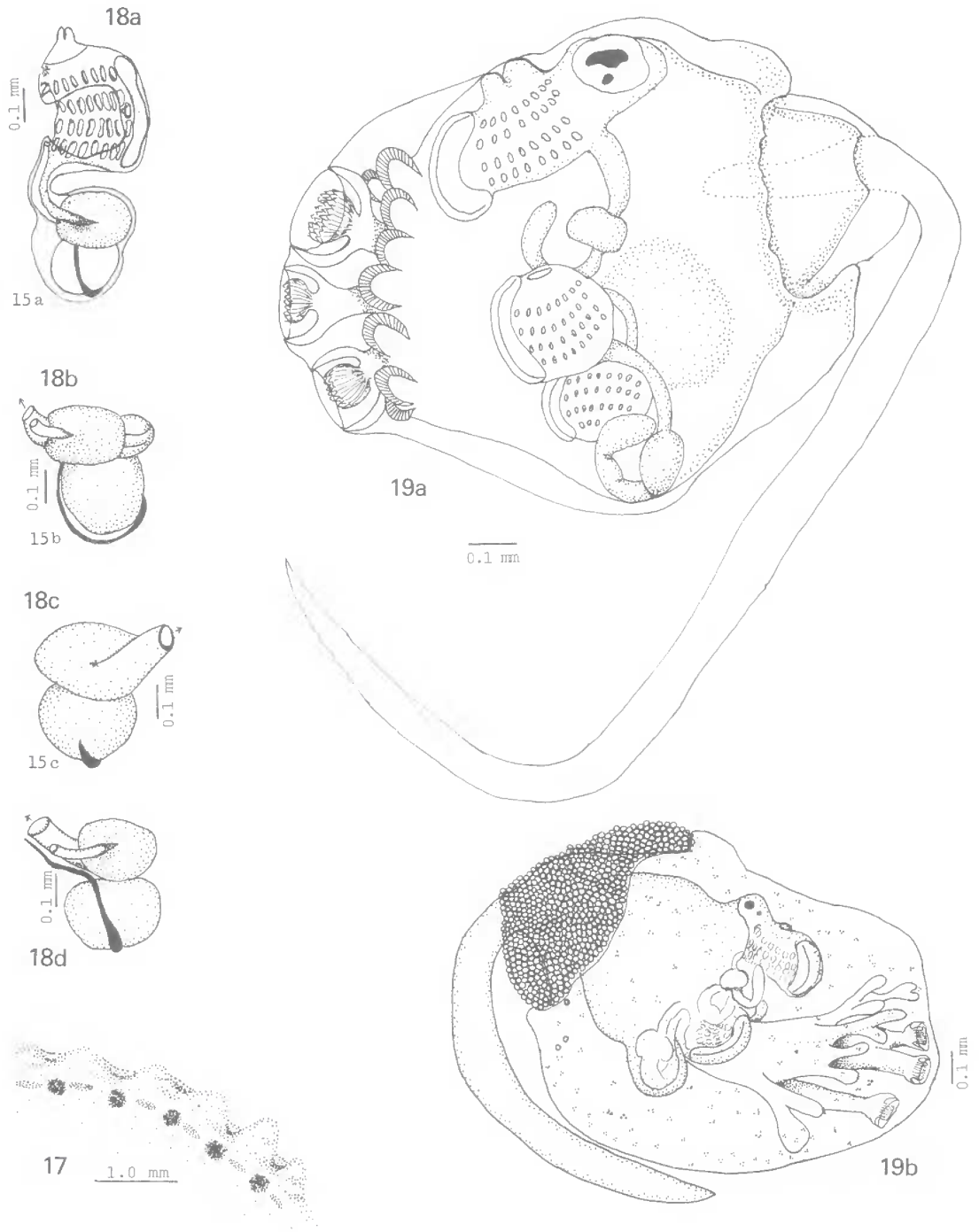
between papillae. Colonies are circular, oval or polygonal flattened cushions up to 4 cm in greatest dimension and up to 5 mm thick. Some of the smaller living colonies appear almost spherical. The borders of the colony are rounded and the test around the periphery of the upper surface is produced into pointed spicule filled conical papillae just outside the peripheral zooid openings. There are occasionally similar papillae from other parts of the upper surface (especially in the colonies from Green I.). The colonies are only loosely attached to the substrate by the basal test. When removed from the substrate the upper surface is depressed and the whole colony seems to contract, the border is elevated and the conical projections around the upper surface become more conspicuous. The colonies from Heron Island are less robust than others, the spicules are relatively sparse in the surface test and it is not produced into conical papillae.

There are one or two cloacal apertures on short tubular projections in the centre of the upper surface. These are made conspicuous by the dense brown pigment in the surrounding test. The branchial apertures are short slits and those around the border are aligned parallel to it. In preserved material these slits are conspicuously green owing to the plant cells that crowd around the branchial sac where it is exposed to the cloacal cavity. Spicules are stellate with 8–12 conical or blunt ended rays in optical section. They are 0·02–0·04 mm in diameter. They are crowded always in the border and in the base of the colony, and usually they are crowded in the surface test and in the test strands that enclose the zooids. In those specimens that are in shaded positions, however, the surface layer of spicules is not dense and the surface of the colony is green owing to green cells in the common cloaca which can be seen through the surface test. Spicules are absent from the area surrounding the cloacal apertures. Cloacal canals perforate the upper layer of test in which the zooids are embedded, and are continuous with voluminous spaces posterior to the zooids.

ZOOIDS: These are crowded in the test. They are about 0·8 mm long. The branchial lobes are reduced to a ventral and dorsal lip and the aperture is a slit. The atrial aperture is wide exposing much of the branchial sac. There are four rows of 8 longish oval stigmata. A deep egg shaped lateral organ projects into the peribranchial space opposite the third row of stigmata at either side of the endostyle. Its attachment to the body wall is narrow so that in section it is comma shaped (Michaelsen 1920). Some very fine muscle fibres extend from the posterior end of the zooid and into the test but these are most inconspicuous and no actual retractor muscle can be demonstrated. The gut loop is short and horizontal. The ♂ gland is undivided and the vas deferens is hooked around it, the proximal end of the duct extending posteriorly from the left side of the follicle, postero-ventrally, and around onto the opposite side where it runs anteriorly along the inner side of the rectum.

LARVAE: These are present in specimens from Fiji in July and a few were present in colonies from Lizard I. on June 1973 (G9913). They were not present in specimens from Green I. (August 1979). Testis follicles appear mature in most specimens. The body of the larva is 1·5 mm long and the short tail is wound only about one third of the distance around it. There are usually three large adhesive organs, rather close together. However, one of these appears to have arisen by subdivision since the two uppermost organs share a basal common stalk. There is a ring of 8 pairs of ampullae around the stalks of the adhesive organs, each with a cap of modified columnar cells. The body of the mature larva contains an oozooid with otolith and ocellus, and two blastozooids. The larval test contains scattered patches of brown pigment cells that are absent only from the area around the posterior end of the body at the base of the tail, where a cap of plant cells adheres in the mature larva. As the larva matures the test appears to be growing back to enclose the posterior end of the larva, together with its adherent plant cells, in a pocket around the base of the tail, that is very likely an incipient cloacal cavity.

REMARKS: Some of the smaller almost spherical living colonies of this species bear a superficial resemblance to *Didemnum molle* in shape and colour. However the cloacal cavity is not so extensive, they lack the copious mucous secretion of *D. molle,* the spicules are relatively large and stellate and the arrangement of pigment, and the conical projections around the border of the colony distinguish them. Those green colonies with less dense spicules in the upper surface are readily distinguished from *L. bistratum* by the form of the spicules and usually by the large spherical pigment cells. The modification of the branchial lobes is also found in *Lissoclinum bistratum* and *L. patellum.*




FIGS. 17–19: *Lissoclinum voeltzkowi* (QM G12474) — 17, part of the border of a colony showing pigment patches (dark shading), branchial apertures, and conical papillae around the borders of the colony; 18, zooid (a, abdomen and thorax; b-d, gut loop and testis from the right, the left, and dorsally, respectively); 19, larva (a, showing test extending posteriorly over area where plant cells are present; b, later larva showing cap of plant cells and pigment patches on test).

Hastings (1931) apparently accepted Michaelsen's interpretation of relationship of the vas deferens in this species with the characteristic spiral duct of the genus *Didemnum*. However its course is characteristic of *Lissoclinum* and is hooked around the posterior border of the gland from the ventral side (against the gut loop) and onto the opposite or dorsal surface. In the genus *Didemnum* the origin of the duct is from the centre of gland on the opposite side.

Both the habitat the appearance of this species over most of its range is most characteristic. Specimens from Heron I. however are few and these have been taken only from cryptic habitats near the eastern end of the reef. Heron I. is possibly at the southern end of the range for the species. The density of spicules in the surface test of these specimens is also much less than most of the specimens further north. The spicules of the surface test undoubtedly protect the colonies from the direct sunlight of the reef flat. Those colonies that occur in shade, or even those parts of a colony that may be curved around the side of a rock into a shaded part of its surface, like the cryptic Heron I. colonies, have fewer spicules in the surface test so that the green plant cells in the cloacal cavity are fully exposed to the light. Light is therefore, possibly an important environmental parameter for this species. Either this factor, or the diurnal temperature range on the reef flat, may preclude its occurrence on the reef flats at the southern end of the Great Barrier Reef.

**Lissoclinum bistratum** (Sluiter, 1905)
(Figs. 20, 21; Plates 2·1a,b)

*Didemnum bistratum* Sluiter, 1905a, p. 103; 1905b, p. 18; 1909, p. 46. Hartmeyer 1909, p. 1449. Michaelsen, 1920, p. 48.
*Didemnum gottschaldti* Tokioka, 1950, p. 118.
*Lissoclinum pulvinum* Tokioka, 1954, p. 247; 1967, p. 97 (part).
*Leptoclinum molle:* Kott, 1962, p. 309; 1966, p. 30.
*Lissoclinum molle:* Tokioka, 1967, p. 95. Kott, 1977, p. 618.
*Didemnum patella:* Millar, 1963, p. 701.
*Didemnum chartaceum:* Kott, 1962, p. 324.

### Material Examined

New Records: Heron I.: October 1979, below low tide amongst rubble near reef edge, QM G12626 (with larvae). SE. Queensland September 1977: Mooloolabah, 18 m on reef slope QM G10108; Mudjimbah, 17 m on reef slope, QM G10125. Green I.: August 1979, rubble zone, QM G12481. Coral Sea (Marion Reef): August 1977, 8 m on top of reef, QM G10170 (AMPI ascidian 204). Fiji (Viti Levu) July 1979: Suva Barrier Reef, in rock pools outer reef flat, LWM, QM G12466; Makaluva, fringing reef, in pools outer reef flat, LWN, QM G12464; Malevu fringing reef, in pools outer reef flat, QM G12467; Tai levu, fringing reef, in pools amongst coral near reef edge, LWM, QM G12483; Deuba, fringing reef, amongst living coral near reef edge, LWM, QM G12581. Palau Is., LWM, QM G12676.

Previously Recorded: *Didemnum bistratum:* Michaelsen, 1920, ZMH K1607, K1108. *Lissoclinum pulvinum:* Tokioka, 1967, USNM 11386, 11396, 11480 (part), 11487, 11538, 11643 (part), 11647, 11663 (part), 11684 (part), 11669 (part), 11678 (part). *Lissoclinum bistratum* > *L. molle:* Kott, 1977, QM G9908 (with larvae), G9911, G9948, G9949 (with larvae), G9950, G9951 (with larvae), G9952.

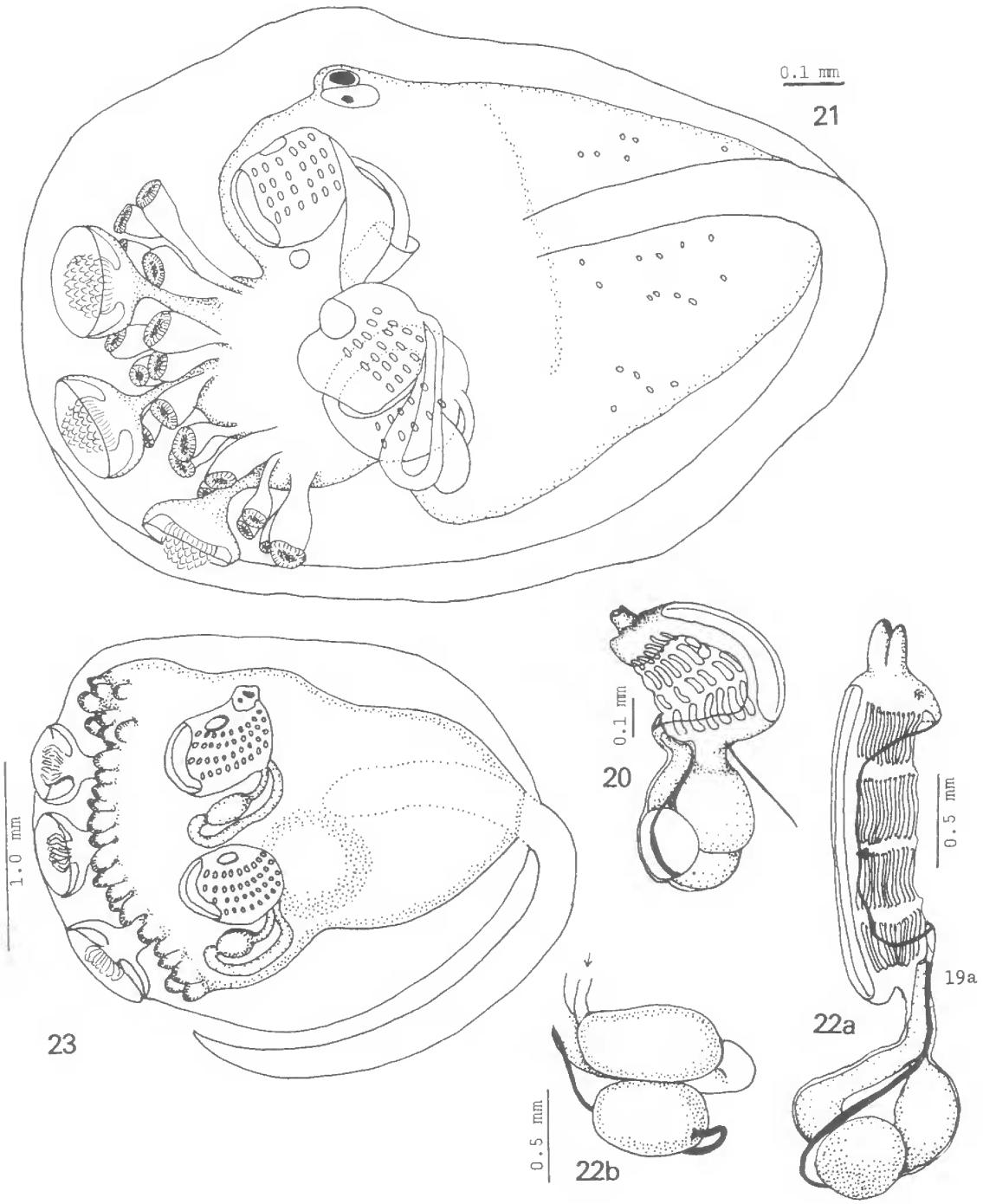
### Distribution

Range: Gulf of Aden (Sluiter 1905a, 1905b). Red Sea (Michaelsen 1920). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I. to Heron I. (Millar 1963; Kott 1962, 1977). SE. Queensland (new records). Indonesia (Sluiter 1909). Japan: Tokara Is (Tokioka 1967). Palau Is (Tokioka 1950). Fiji: Viti Levu (new records).

Habitat: The species is taken in cryptic habitats with *T. cyclops* from just below the low water mark in the outer reef flat and in the rubble zone behind the reef crest. Macroscopically it resembled *T. cyclops,* with which it is often confused.

### Description

Colony: The colonies are small oval cushions or irregular investing sheets, never more than 5 mm thick. They seldom exceed 2 cm, but sometimes are as much as 5 cm in length (specimens from Mooloolaba QM G10108, G10125). Sometimes the common cloacal aperture is sessile, but it is often raised off the surface of the colony on a cylindrical projection, which may lie over the surface, presumably in the direction of the current flow (see Tokioka 1967). They are grey green on the upper surface. The green plant cells in the common cloacal cavity are visible through the surface test. There is usually a layer of bladder cells superficially. Spicules are dense in the borders, and in the basal test. They are often less dense at the level of the abdomina.




FIGS. 20–21: *Lissoclinum bistratum* (QM 12626) — 20, zooid; 21, larva.

FIGS. 22–23: *Lissoclinum patellum* (QM G9930, zooid; AM Y1335, larva) — 22, zooid (a, from the left latero-dorsal aspect; b, abdomen from the right); 23, larva.

Spicules are evenly distributed in the surface test beneath the bladder cell layer, but their concentration varies from colony to colony and in some specimens they completely occlude the bladder cell layer. There are usually spicules associated with the branchial openings and when the zooids are contracted these are drawn down into the branchial siphon in a thick plug. The spicules are 0·03–0·05 mm in diameter. They are spherical, with many crowded blunt ended rays. The test is relatively delicate in this species. Black or reddish pigment is present in the bladder cell layer and sometimes in the body walls of the zooids. Zooids are most often white with a yellow stomach. The branchial lobes are reduced to a ventral and a dorsal lobe and the apertures appear as slits on the surface of the colony as in *L. voeltzkowi*. The zooids are surrounded by thoracic common cloacal cavities which connect with posterior abdominal spaces, although these are often quite restricted. The basal test is relatively thick.

ZOOIDS: These are about 0·9 mm long. The atrial aperture is wide and open exposing most of the branchial sac. There is a deep vertical egg shaped lateral organ projecting into the peribranchial cavity on either side of the endostyle (near the border of the atrial aperture), between the second and third rows of stigmata. There are 6 to 8 long and rectangular stigmata in each row. The gut loop is simple and vertical. The ♂ gland is undivided and the vas deferens is hooked around the posterior end of the gland.

LARVAE: These are present in colonies from Darwin in October 1965 and from Heron I. in December (QM G9951), January 1976 (QM G9949), March 1975 (G9908 and October 1979 (QM G12626). Colonies from Fiji had some large eggs but no embryos in July (G12581). The species may breed all the year with a peak in early summer.

The large body is about 1 mm long the tail is wound half way around it. There are 3 large adhesive organs surrounded basally by 8 pairs of ectodermal ampullae. There is an oozooid and two blastozooids. The 'pouch' referred to by Kott (1977) is actually the posterior extension of the posterior haemocoelic cavity, with a layer of ectoderm and test outside it. The posterior cap of algal cells adhere to the larval test in this region to form the posterior cap, around the base of the tail described by Kott *(loc. cit.)*. The cells at tips of the 8 pairs of conspicuous ectodermal ampullae are modified columnar cells and form a concavity on the end of each ampulla.

REMARKS: The species is very closely related to *L. voeltzkowi*, which has a similar (though more extensive) cloacal cavity, similar zooids, lateral organ, branchial sac, gut loop, and larva. In its more characteristic form the colony of *L. voeltzkowi* is readily distinguished from *L. bistratum*. However in cases where spicules are not dense in the surface test of *L. voeltzkowi* or when they are dense in the surface test of *L. bistratum* the spicules constitute a reliable means to distinguish the species.

This species has been reported further to the south than has so far been recorded for any other algal-bearing didemnid.

**Lissoclinum patellum** (Gottschaldt, 1898)
(Figs. 22, 23; Plate 2·2)

*Didemnoides patella* Gottschaldt, 1898, p. 653.
*Didemnoides sulcatum* Gottschaldt, 1898, p. 651.
*Didemnoides ternatanum* Gottschaldt, 1898, p. 648.
*Didemnum patella:* Michaelsen, 1920, p. 63. Tokioka, 1950, p. 115. Millar 1975, p. 228.
*Leptoclinum patella:* Kott, 1962, p. 310.
*Lissoclinum patella:* Tokioka, 1967, p. 97. Kott, 1977, p. 619.
*Diplosomoides tropicum* Sluiter, 1909, p. 88.
*Didemnum meandrium* Sluiter, 1909, p. 64.
Not *Didemnum ternatanum:* Kott, 1977, p. 618 and synonyms (< *D. molle*).
Not *Didemnum patella:* Millar, 1963, p. 701 (< *L. bistratum*).

MATERIAL EXAMINED

NEW RECORDS: Swain Reefs: October 1974, reef slope, QM G9930. Heron I.: November 1978, reef slope, QM G1190. Palau Is., QM G12679.

PREVIOUSLY RECORDED: *Didemnoides patella* Gottschaldt, 1898, Holotype ZMH K1087. *Lissoclinum patella:* Tokioka, 1967, USNM 11419, 11637, 11664, 11688; Kott, 1962, AM Y1335 (with larvae); 1977, QM G9278, G9456, G9887. *Didemnoides ternatanum* Gottschaldt, 1898, Holotype ZMH 595. *Lissoclinum tropicum:* Van Name det., AMNH Chordata 2143. *Didemnum maeandrium* Sluiter, 1909, Syntypes ZMA TU.459, TU.457.

DISTRIBUTION

RANGE: Western Australia: Pt. Peron, Rottnest I. (Kott 1962). Great Barrier Reef: Heron I., Swain Reefs (Kott 1962, 1977). Indonesia (Gottschaldt 1898, Sluiter 1909, Millar 1975). Borneo (Sluiter 1909). Palau Is. (Tokioka 1950, 1967).

HABITAT: The species is one of the few plant bearing didemnids that does not occur intertidally. It is taken on vertical surface and under ledges from very shallow water to about 10 m. Larger specimens are taken only from deeper water. The species is large and robust and it is unlikely that adequate attachment to the substrate could be effected unless the substrate was free of sediments.

DESCRIPTION

COLONY: Large colonies up to 1 cm in thickness. They have firm rounded gelatinous ridges on the surface. Cloacal and zooid openings are between these ridges. The basal test is also firm and gelatinous and as thick as the surface ridges. Small colonies consist of a single system that is surrounded by a ridge of gelatinous test around a central depressed area. Subsequently raised surface swellings develop (Tokioka 1967) and in due course assume the characteristic facies of the larger colonies (see Millar 1975, fig. 20). The thin zooid layer is conspicuous owing to the plant cells that fill the common cloacal cavity that surrounds the zooids and extends posterior to them. Spicules are also present in the zooid layer of test. They are characteristically spherical, and have a large size range, from 0·01 to 0·08 mm in diameter.

ZOOIDS: These are large. There are 4 rows of 14 very elongate stigmata. There are very fine muscle fibres in the transverse vessels that fan out either side of the endostyle and form circular bands around each zooid. There do not appear to be any longitudinal fibres along the dorsal or ventral borders of the pharynx and there is no retractor muscle. The long rectangular stigmata are almost completely exposed and the peribranchial cavity is almost completely lost, a narrow strip along either side of the endostyle being all that remains of the outer body wall. There is a small egg-shaped lateral organ projecting inwards between the second and third rows of stigmata. The two lobes of the branchial siphon, each with longitudinal muscle fibres that curve toward each other in the border, are marked by clumps of spicules where they are inserted into pockets of test. The oesophagus is long and the stomach and intestine form a simple loop that is flexed ventrally at an angle to the thorax. The single egg shaped ♂ follicle lies in the usual position beneath (or dorsal to the loop of the gut). The proximal end of the vas deferens is from the right side almost at the end of the gland, and extends in a slight loop around on to the dorsal side of the gland to extend anteriorly alongside the rectum.

LARVAE: These are present only in colonies from Point Peron in January 1948 (AM Y1335). There are mature ♂ follicles and sperm-filled vas deferens in Swain Reefs specimens of October, 1974 (QM G9930). Neither mature gonads nor larvae were present in large colonies from Heron I. in either March or December.

The larvae are large and almost spherical, 2·5 mm. The adhesive organs have unusually short stalks and the adhesive cone and surrounding ectodermal cup are unusually shallow. There is a single blastozooid unlike the larvae of *L. voeltzkowi* and *L. bistratum* which have two. There are plant cells around the posterior end of the larva outside the posterior haemocoelic chamber. There is also an unusually large number of ectodermal ampullae (about 15 pairs) with a rounded cap of modified columnar ectodermal cells on the tip of each.

REMARKS: Michaelsen (1920) interpreted the course of the vas deferens as an incipient spiral. However, unlike *Didemnum* spp. the ascending part of the vas deferens is on the opposite side of the gland to its point of origin. Its relationship to other species of the genus *Lissoclinum* rather than *Didemnum* is also unmistakable in respect of other characters. The cloacal system, the presence of blastozooids in the larvae, the modification of the branchial lobes, the virtual loss of the peribranchial cavity, the absence of a retractor muscle and the long narrow stigmata all resemble the condition observed in *L. voeltzkowi, L. bistratum* and, with the exception only of the branchial lobes, *L. punctatum*. It is distinguished from all others by the great range in the size of the spicules and by the solid thick gelatinous colony that it forms. Although the larval form has similarities with the other *Lissoclinum* spp. above, it is also distinguished by its greater size.

*Didemnoides ternatanum* Gottschaldt is described with a coiled vas deferens. An examination of the type in the Hamburg Zoologisches and Staats Institut Museum has shown it to be a small colony of the present species.

This is the most robust of the plant-bearing didemnids, and with *Didemnum molle,* is found at greater depths than is usual for this group of species. Despite the greater depth at which the species is found, the plant cells are further screened from light by the high gelatinous translucent ridges on the upper surface.

### **Lissoclinum punctatum** Kott, 1977
(Figs. 24, 25; Plate 2·3)

*Lissoclinum punctatum* Kott, 1977, p. 620.
*Lissoclinum molle:* Newcomb and Pugh, 1975, p. 533.

MATERIAL EXAMINED

NEW RECORDS: Green I.: August 1979, amongst rubble near reef edge, LWM, QM G12456. Nelly Bay, Magnetic I.: August 1978, QM G11916. Heron I.: October 1979, cryptic, in pools below LWM near reef edge, QM G12624. Fiji, Viti Levu, July 1979: Vuda Pt. fringing reefs in pools outer reef flat, QM G12451 (with embryos); Malevu, fringing reefs in pools, outer reef flat, QM G12452, (with embryos); Makaluva reef, in pools, outer reef flat, QM G12462.

PREVIOUSLY RECORDED: *Lissoclinum punctatum* Kott, 1977, Holotype QM G9920; Paratypes QM G9426, G9926. *Lissoclinum molle:* Newcomb and Pugh, 1975, QM G8592.

DISTRIBUTION

RANGE: Great Barrier Reef: Lizard I., Green I., Heron I. (Kott 1977; new records). Fiji: Viti Levu (new records).

HABITAT: The species is found just below low tide, in cryptic habitats, usually on coral skeletons.

DESCRIPTION

COLONY: These are small, investing and very thin. They are bright green, with capsules of white spicules around each zooid. These are clearly seen through the test. The colonies are very soft and often disintegrate into a stream of mucus where attempts are made to scrape them from the substrate. In life, the plant cells are contained in common cloaca. However the test disintegrates so readily when the colony is disturbed that they are often found mixed with the test in the preserved material. There may be some dark spherical pigment cells in the surface test. The common cloacal cavity is large and extends posterior to the zooids but only occupies the upper half of the colony. The lower half consists of basal test. Spicules are present only in the capsules that surround the zooids, mature ova and embryos. They are spherical, 0·01–0·03 mm in diameter and are composed of radiating flat ended rods.

ZOOIDS: The zooids are small and each is completely enclosed in a capsule of spicules. The branchial aperture has 6 shallow lobes. The atrial aperture is wide exposing most of the branchial sac. There is a small, comma-shaped lateral organ from either side of the endostyle between the second and third rows of stigmata. There are about 8 long narrow stigmata in each of the 4 rows. Fine muscle fibres from the thorax extend down onto the oesophageal region but do not form a retractor muscle. The gut loop is simple and horizontal. There is a straight vas deferens that hooks around the posterior end of the single ♂ follicle at its proximal end.

LARVAE: Mature eggs and some tailed embryos are present in specimens from Malevu and Vuda Point (QM G12451 and G12452) in July 1976 and mature ova were present at Green I. in August, 1976 (G12456). Other colonies taken in May, August and September at various locations on the Great Barrier Reef did not contain mature gonads. However, the fact that these small colonies are present at all suggests that breeding may occur throughout the year. The tailed embryos are large (0·6 mm) and the tail is wound right around the larval trunk. They are not sufficiently well developed, however, to determine their structure. No blastozooids can be distinguished, although the larval thorax is very small and the developing oesophageal neck is long as in *L. voeltzkowi, L. bistratum* and *L. patella,* all of which do have larval blastozooids. However, the yolk mass is anterior to the developing oozooid as in other species in which there is no larval blastozooid. (In those larvae with buds the yolk mass is always posterior to the oozooid and its buds).

REMARKS: The zooid of this species is similar to others in the genus *Lissoclinum.* It is characterised by the small very soft colony and the capsule of small spherical spicules around the zooid. The 6 branchial lobes distinguish it from the three lissoclinid species discussed above in which the branchial lobes are modified.

### **Echinoclinum triangulum** (Sluiter 1909)
(Fig. 26; Plate 2·4)

*Diplosomoides triangulum* Sluiter, 1909, p. 86.
*Lissoclinum triangulum:* Kott, 1977, p. 620.
*Echinoclinum triangulum:* Millar, 1975, p. 241.
*Echinoclinum philippinensis* Tokioka, 1967, p. 93.

MATERIAL EXAMINED

NEW RECORDS: Heron I.: October 1979, cryptic below LWM near reef edge, QM 12623.

PREVIOUSLY RECORDED: *Lissoclinum triangulum*: Kott, 1977, QM G9466, G9793, G9932. *Echinoclinum philippinensis* Tokioka, 1967, Types USNM 11791, 11790.

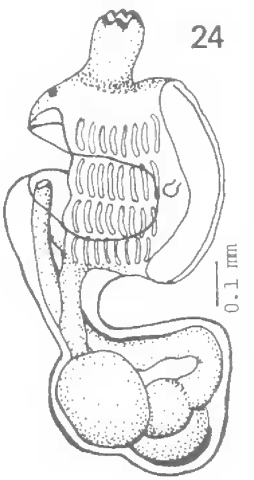
## DISTRIBUTION

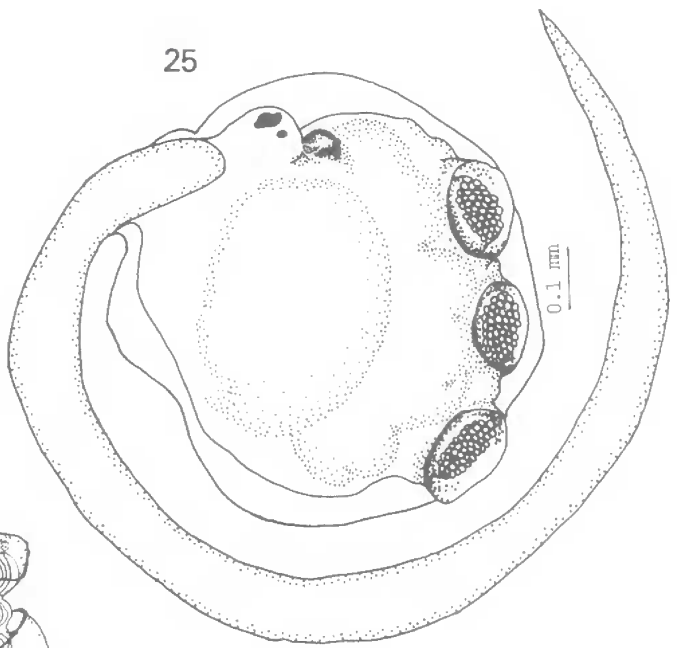
RANGE: Indonesia: Saleyer, Amboina (Sluiter 1909, Millar 1977). Philippines (Tokioka 1967). Great Barrier Reef: Heron I. (Kott 1977).

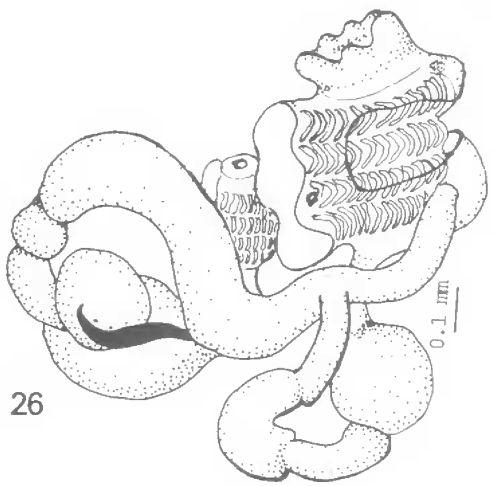
HABITAT: The species occupies cryptic habitats in the rubble zone, and on the edge of the reef below the low water mark down to 20 m.

## DESCRIPTION

COLONY: The colonies are flat, soft, and yellowish green. Most records are of colonies less than 1 cm in length. One specimen from Heron Island at 20 m (G9466) is 6 cm long and 0·5 cm thick. There are spherical brown pigment cells in the test and the body walls of the zooids in some of the larger specimens. The whole test is filled with larger bladder cells. Beneath the superficial layer of test there is (in the larger colonies) a layer of spicules that become increasingly sparse towards the base. Spicules are always more common around the zooids, and in the smaller colonies the spicules are absent from the remainder of the test and only form a sparse coat around the zooids.




FIGS. 24–25: *Lissoclinum punctatum* (QM 12452) — 24, zooid; 25, embryo.

FIG. 26: *Echinoclinum triangulum* (QM G9466) — zooid with blastozooids.

The spicules are made up of fine pointed rays of varying length, grouped together to form a thickened central area that gradually flattens toward the periphery, where it is drawn out into 3–6 points, sometimes resembling the outline of a small asteroid echinoderm. The spicules are 0·03 to 0·08 mm in greatest diameter (from point to point). The secondary common cloacal cavity between the zooids is thoracic. However a very extensive posterior abdominal space extends to the surface around large groups of zooids that are joined to the basal test by a single test connective crossing the posterior abdominal cavity. Plant cells are present in the test and in the common cloacal cavity.

ZOOIDS: The thorax and abdomen are each about 0·5 mm in length and the abdomen is bent up alongside the thorax. There are 6 shallow branchial lobes and a distinct sphincter muscle. The atrial aperture is wide and exposes most of the branchial sac when it is extended. There are 4 rows of 12 very delicate narrow elongate stigmata. There is a small narrow lateral organ that projects inwards on either side of the endostyle between the second and third rows of stigmata. There is no retractor muscle. The gut forms a straight simple loop. In freshly preserved material the stomach and the corresponding (glandular) part of the ascending limb of the intestine are clear yellow. The proximal part of the vas deferens extends anteriorly from the mid-dorsal surface of the single ♂ follicle. It is not hooked around the posterior border of the gland from its ventral side as is usual in *Lissoclinum*.

LARVAE: Although specimens from Heron I. taken in December have mature ♂ follicles no colonies have yet been taken from the Great Barrier Reef with mature ♀ gonads. Colonies without mature gonads have been collected in September and October at Heron I.

Millar (1975) found larvae in the base of one of the colonies he examined. They are 0·45–0·6 mm with a deep, almost spherical trunk and a short slender tail wound only about one third of the distance around the larval trunk. The adhesive organs have very slender stalks and shallow ectodermal cups. There are 6 ectodermal ampullae, two on each side of the base of the stalks of the adhesive organs and a dorsal and ventral ampulla. The cells on the tips of the ectodermal ampullae appear to be modified. The larval thorax is large and there are no blastozooids. There is an anterior yolk mass at the base of the ampullae.

REMARKS: The origin of the straight vas deferens from the mid dorsal surface, is the same as in *Echinoclinum verilli*. The present species and *E. verilli* are accordingly afforded a generic status that is distinct from the closely related *Lissoclinum*. A vas deferens of this type has also been described for *Diplosoma handi* Eldredge 1967 (see below: *D. virens*).

The present species is also distinguished by the presence of plant cells in the test, the form of the spicules, the thoracic cloacal system, and the orientation of the abdomen that is flexed up against the thorax. The larva is also different from *Lissoclinum* larvae, having no blastozooids, a deep larval trunk, deep thorax, very slender adhesive organs and stalks, an anterior yolk mass and few ectodermal ampullae. Kott (1977) mistakenly recorded 2 ♂ follicles. The testis is undivided in this species.

**Diplosoma virens** (Hartmeyer, 1909)
(Figs. 27–30)

*Diplosoma viride* Herdman, 1906, p. 341.

*Leptoclinum virens* Hartmeyer, 1909, p. 1456. Tokioka 1943, p. 500; 1967, p. 68. Kott, 1966, p. 291.

*Diplosoma virens:* Hastings, 1931, p. 102. Newcomb and Pugh, 1975, p. 533. Thinh and Griffiths, 1977, p. 673. Thinh, 1978, p. 617.

*Leptoclinum simile* Sluiter, 1909, p. 77 (part).

*Leptoclinum varium* Sluiter, 1909, p. 80.

*Leptoclinum calificiforme* Sluiter, 1909, p. 82. Van Name, 1918, p. 160

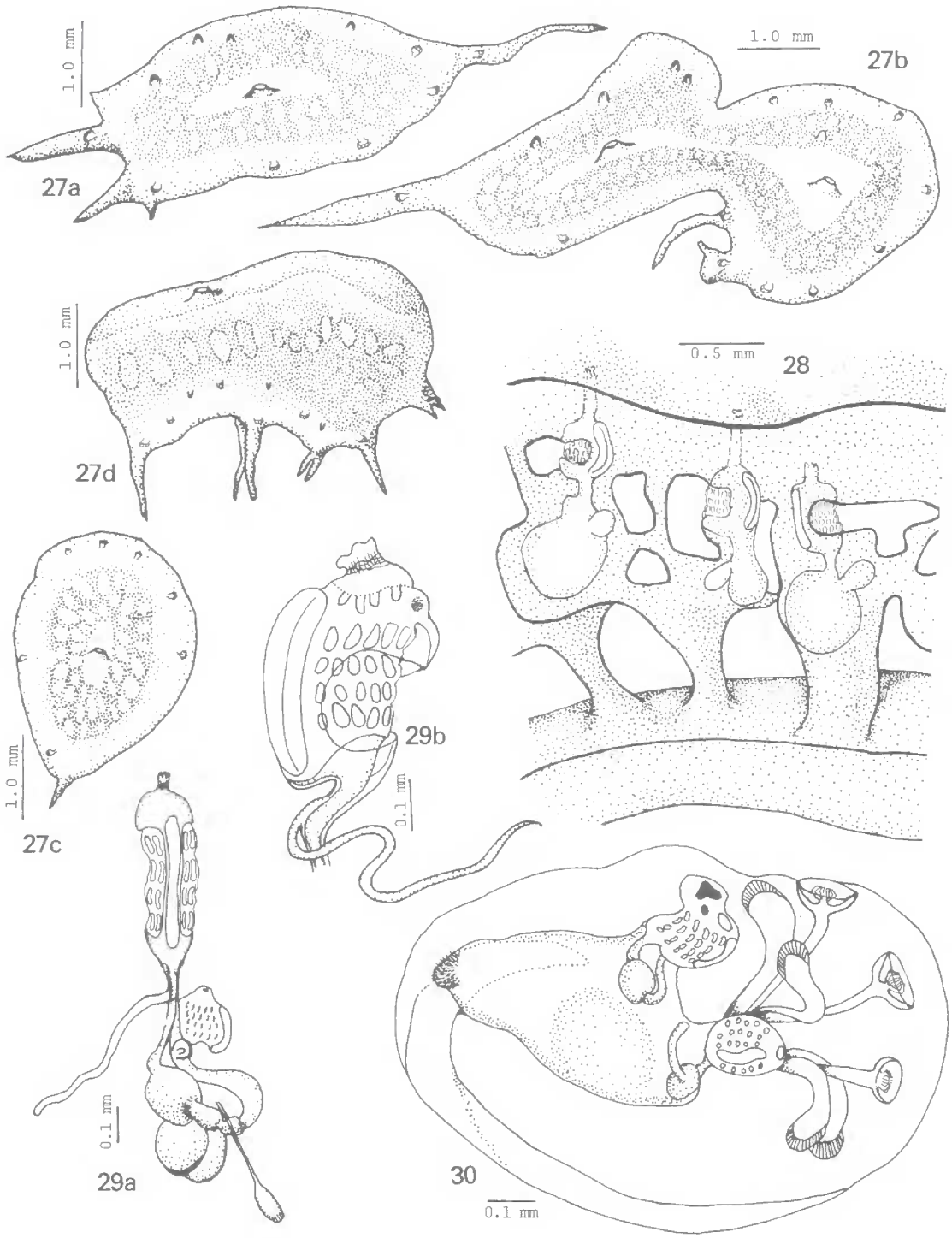
Not *Leptoclinum viride* Herdman, 1906, p. 34 (< *Didemnum viride*)

Not *Diplosoma virens:* Eldredge, 1967, p. 228. Kott, 1977, p. 620. Thorne, Newcomb and Osmond, 1977, p. 575. (< *Diplosoma similis*).

MATERIAL EXAMINED

NEW RECORDS: Heron I.: October 1979, cryptic, below LWM near edge of reef, QM G12631. Green I.: August 1979, inner sandy reef flat on *Halimeda,* QM G12484. Fiji (Viti Levu) July 1979: Vuda Point, fringing reef, in pools, outer reef flat, QM G12486; Malevu, fringing reef, in pools behind cascades and on inner sandy reef flat, QM G12485 (some larvae); Makaluva reef, inner sandy reef flat, QM G12461.

PREVIOUSLY RECORDED: *Diplosoma viride* herdman, 1906, Holotype BM 1907.8.30.42. *Diplosoma virens:* Newcomb and Pugh, 1975, QM G8593; Kott, 1977 (Heron I.), QM G9797, G9445, G9882, G9888, G9937 (with embryos); Kott, 1966 (Darwin), AM 1119 (with larvae) *Leptoclinum varium* Sluiter, 1909, Syntypes ZMA TU.599.6, TU.599.8, ZMA TU.597. *Leptoclinum calciforme* Sluiter, 1909, Holotype ZMA TU.573. *Leptoclinum simile* Sluiter, 1909, Syntype ZMA TU.591.2 (with larvae).




FIGS. 27–30: *Diplosoma virens* (QM G1285, colonies; QM G12484, zooids; QM G9937, larva) — 27, colonies (a–c, upper surface; d, side view); 28, section through part of a colony; 29, zooid (a, with extended thorax; b, contracted thorax); 30, larva.

## Distribution

Range: Ceylon (Herdman 1906). Northern Australia (Kott 1966). Great Barrier Reef: Lizard I., Low Is., Green I., Heron I. (Hastings 1931, Kott 1977). Indonesia (Sluiter 1909). Palau Is., Gilbert Is., Philippine Is., Marshall Is (Van Name 1918, Tokioka 1967). Fiji: Viti Levu (new records).

Habitat: The greatest depth recorded for this species is from off Amboina at 40 m (ZMA TU.599.6) and there are other records from similar depths. It is also found often on the open reef flat and around the sides of pools and on weed where it is just covered with water at low tide. At Heron Island the colonies are larger than is usual for the species, and are found along the reef edge and in surge channels amongst strands of living coral down to 5 m.

## Description

Colony: The usual appearance of the living colonies is very adequately described by Herdman (1906, p. 341): '. . . . numerous small rounded colonies closely placed . . . . The centre of the colony where the common cloaca is placed is depressed and of a paler green colour. The zone of ascidiozooids is also paler, while the outer ring of the colony, outside the ascidiozooids is the darkest and is usually of a very rich green colour.' The living colonies are rounded egg-shaped or almost spherical. They closely resemble the sea-weed, *Caulerpa,* with which they are often associated. The depression is the centre of the upper surface that is referred to by Herdman is present only in contracted or preserved specimens. In larger specimens this depression causes the colonies to assume the 'saucer' shape described by Sluiter (1905) for *D. caliciforme.* The preserved specimens are yellowish mustard-green grey or brownish-yellow and opaque. The colonies are oval, up to 1 cm long and 2–5 mm thick. Colonies on the reef edge, in surf channels, at Heron I. are up to 2 cm long and about 5 mm thick. The common cloacal aperture, from the centre of the upper surface, is on a conical or occasionally a cylindrical protruberance. The latter may be bent over, to lie more or less flat over the surface of the colony, with the upper rim incised in a V extending back along the surface of the cylinder. The borders of the colonies are vertical and rounded. Zooids may be numerous, arranged fairly densely around the central area, but are often in a single circle around the periphery of the colony. The colonies are only loosely attached to the substrate by a small area of the lower surface, or by numerous slender test extensions from the under surface, or from around the border or by a stout, stalk-like extension of the test from the centre of the under surface. Many of the colonies are irregularly shaped and appear to be dividing. Such a growth pattern would explain the dense aggregations that are so characteristic of the species. The colonies are quite firm and the test is very tough and apparently fibrous. There is a surface layer of bladder cells. Beneath this, the fibrous test in which the zooids are embedded is perforated by a network of rather narrow interconnecting cloacal canals that open into a more extensive basal cavity that is posterior to the zooids and traversed by short basal test connectives that anchor large groups of zooids to the base of the colony. The colony is thus divided horizontally into four layers all of approximately equal thickness, viz.: the surface test, the zooid bearing layer perforated by a network of narrow canals, the posterior abdominal cloacal cavities, and the basal test. These layers are present in even the smallest colonies. The complicated network of thoracic canals, and the tough, rigid colonies cause the plant cells to remain trapped inside the preserved colonies and contribute to the opacity of the colonies. They are translucent only in the depressed central area where the cloacal cavity lies beneath the central aperture. The zooids can be removed from their tough test sheaths only with the greatest difficulty. Stolonic vessels extend from the abdominal regions of the zooids into the test connectives and especially into the basal test around the periphery of the colony.

Zooids: In the preserved material the zooids are whitish with clear yellow stomach and glandular portion of the intestine. Sometimes there is some brown pigment in the abdominal body wall. Zooids are small, about 1 mm long. The thorax and abdomen are of equal length. There is active budding from the neck, with up to two sets of blastozooids present at the one time. The oesophageal neck is often very long. There are 5–6 rounded to oval or elliptical stigmata in each of the 4 rows. The stigmata are lined by rather flat epithelial cells. The atrial aperture is very wide, exposing most of the branchial sac. The branchial siphon is quite narrow with a pronounced sphincter muscle. There is a long retractor muscle that is free from about half way down the

oesophageal neck. The thoracic musculature between the rows of stigmata and extending into the retractor muscle from the dorsal and ventral borders of the zooid, is fine but conspicuous. The abdomen forms an angle with the thorax and is flexed from the base of the oesophagus. The stomach is roomy and elongate. There are two ♂ follicles dorsal to the gut loop and a single straight vas deferens swollen and proximally hooked around the posterior border between the two lobes of the gland.

LARVAE: Larvae were present in colonies from Darwin in October 1965 (Kott 1966). A few were present in colonies from Heron I. in March 1975 and from Malevu in July 1979 and from the Celebes in January 1900. They are large, the larval trunk being slightly more than 1 mm long. The tail is wound about three quarters of the way around the trunk. There are usually three large median adhesive organs (one embryo was observed to have only two). There are two thick pairs of ectodermal ampullae, with modified columnar cells around their free ends. The oozooid has a large otolith and ocellus. There is a single blastozooid. In mature larvae there is a deep division between the oozooid and blastozooid. The latter remains associated with the frontal stalk from which the ectodermal ampullae and the adhesive organs arise.

In each of the *Diplosoma* species with algal symbionts there is an identical organ for the transference of plant cells from the parent colony. The name *rastrum* is suggested for the organ. In the specimens from Darwin it has not evolved beyond the stage where it is a bilateral swelling of the posterior haemocoelic chamber above the base of the tail but in the specimens from the Celebes (ZMA TU.591.2) it reaches its full development. It first appears as bilateral outgrowths of the postero-dorsal part of the posterior haemocoelic chamber, either side of the mid line above the base of the tail. The ectoderm on these swellings is modified and produced into minute scale-like projections similar to those observed on the ectoderm covering the whole posterior haemocoelic chamber in *Didemnum molle*. As the embryo matures, the bilateral swellings become continuous across the mid line and the whole postero-dorsal aspect of the larva is constricted off from the larval trunk as a more or less cylindrical transverse arc with anteriorly curving horns at either end. A narrow median stalk from that part of the larval trunk over the base of the tail supports the organ. Its central cavity is continuous with the posterior haemocoelic chamber. The test over it is differentiated into a mass of very fine threads with terminal swellings that entangle the plant cells. As the tail is withdrawn into the posterior haemocoelic chamber, the rastrum is pulled into the larval test, which also overgrows it and its adherent plant cells as the cloacal cavity of the colony is formed. This parallels the process in *Tridemnum paracyclops* (see above).

REMARKS: The species is closely related to *Diplosoma similis* with which it has often been confused. The most conspicuous distinction is the shape, consistency, size and form of attachment of the colony, and the form of the common cloacal system. The zooids of *D. virens* are smaller and more narrow than those of *D. similis* and the stomach is shorter. *D. virens* larva has two pairs of ectodermal ampullae instead of three. The species occupy different habitats at low latitudes although at Heron I. they are often taken together.

In his description of *Leptoclinum varium* Sluiter has not mentioned the presence of plant cells, however it is possible that he mistook these for what he reports as numerous blood corpuscles. Although the branchial siphon in the present specimens is much shorter than that figured by Sluiter, this character varies with the thickness of the surface layer of test. It is also affected by the degree of contraction of this rather muscular organ. One of the syntypes of *L. simile* (Sluiter 1909) is also identical with the present species and also contains plant cells, confirming the identification. It is possible that in these specimens plant cells were mistaken for pigment cells.

The colonies of *Diplosoma handi* Eldredge, 1967 from the Caroline Is. resemble this species in their size, thickness, tough solid test, high cloacal apertures and the presence of vascular stolons in the thick basal test. They are distinguished by the absence of the posterior abdominal portion of the cloacal cavity. In this and other characters they resemble *D. similis*. The course and position of the gut loop, bent up alongside the thorax, the restricted cloacal cavity, the long branchial siphon and the vas deferens (which appears to extend anteriorly from the centre of the dorsal surface of the single ♂ follicle and is not hooked around from the other surface of the gland) are all reminiscent of *Echinoclinum triangulum*.

**Diplosoma similis** (Sluiter, 1909)
(Figs. 31–33)

*Leptoclinum simile* Sluiter, 1909, p. 77.
*Diplosoma virens:* Eldredge, 1967, p. 228. Millar, 1975, p. 241. Kott, 1977, p. 620 (part). Thorne, Newcomb and Osmond, 1977, p. 575.

MATERIAL EXAMINED

NEW RECORDS: Green I.: August 1979, outer reef flat on rubble, QM G12480. Fiji, Viti Levu, July 1979: Deuba, in pools, reef edge, LWM, QM G12013 (turquoise colour), QM G12014 (green colour), QM G12450 (teal blue colour); Malevu, in pools behind reef crest, QM G12454 (with larvae); Makaluva in pools behind reef crest, LWM, QM G12465; Tailevu, in crevasses near reef edge, LWM, QM G12006; Suva Barrier Reef, in pools near reef edge, LWM QM G12456; Serua in depression in sandy Reef flat, LWM, QM G12012. Line Is., Christmas I.: February 1979, on reef flat, QM G12010 (with larvae).

PREVIOUSLY RECORDED: *Diplosoma virens:* Kott 1977, QM G9924, G9789 (Lizard I.); G9923 (Townsville, Magnetic I.); G9795, G9880, G9883 (with larvae), G9884, G9885, G9886, G9889, G9933, G9934, G9935, G9936, G9938, G9939, G12634, G12635, G12636, G12637 (Heron I.). *Leptoclinum simile* Sluiter, 1909, Lectotype ZMA TU.591.1.

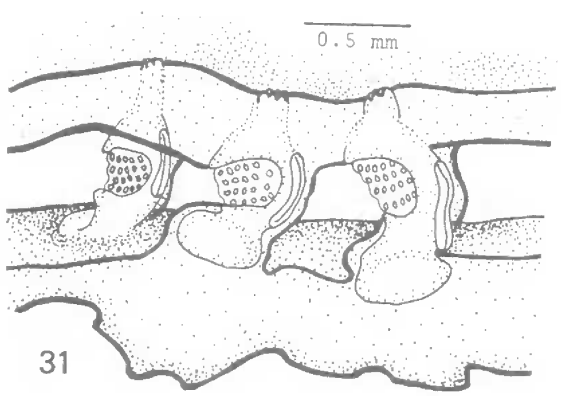
DISTRIBUTION

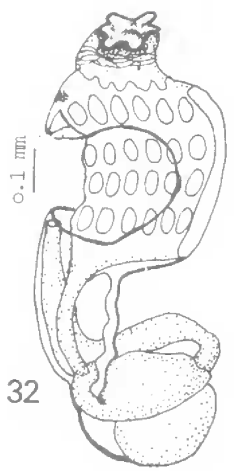
RANGE: Great Barrier Reef: Lizard I. to Heron Is. (Kott 1977). Indonesia (Sluiter 1909). Eniwetok, Mashall Is., Hawaii (Eldredge 1967). Line Is.: Palmyra (Eldredge 1967), Christmas I. (new records). Fiji: Viti Levu (new records). Philippines (Millar 1975). ? Japan: Tokara Is. (Tokioka 1954).

HABITAT: The species is usally found near the edge of reefs where it binds together the rubble (including coral skeletons) that collects in pools and crevices. At Heron Island it is seldom exposed directly to the light but occupies more cryptic habitats deeper down amongst the rubble. At lower latitudes, including Fiji, Low Isles and Darwin it is often found directly exposed to the light, lining the sides of pools behind the reef crest.

DESCRIPTION

COLONIES: These form thin encrusting sheets that are often very extensive. They adhere closely to the substrate by the whole of their basal surface, and their surface contours are irregular, corresponding with the contours of the substrate. They are seldom more than 2 mm thick. Their growth is not limited by the size of the substrate, for around the borders of the colony it often




FIGS. 31–32: *Diplosoma similis* (QM G9883) — 31, cross section through a colony; 32, zooid.

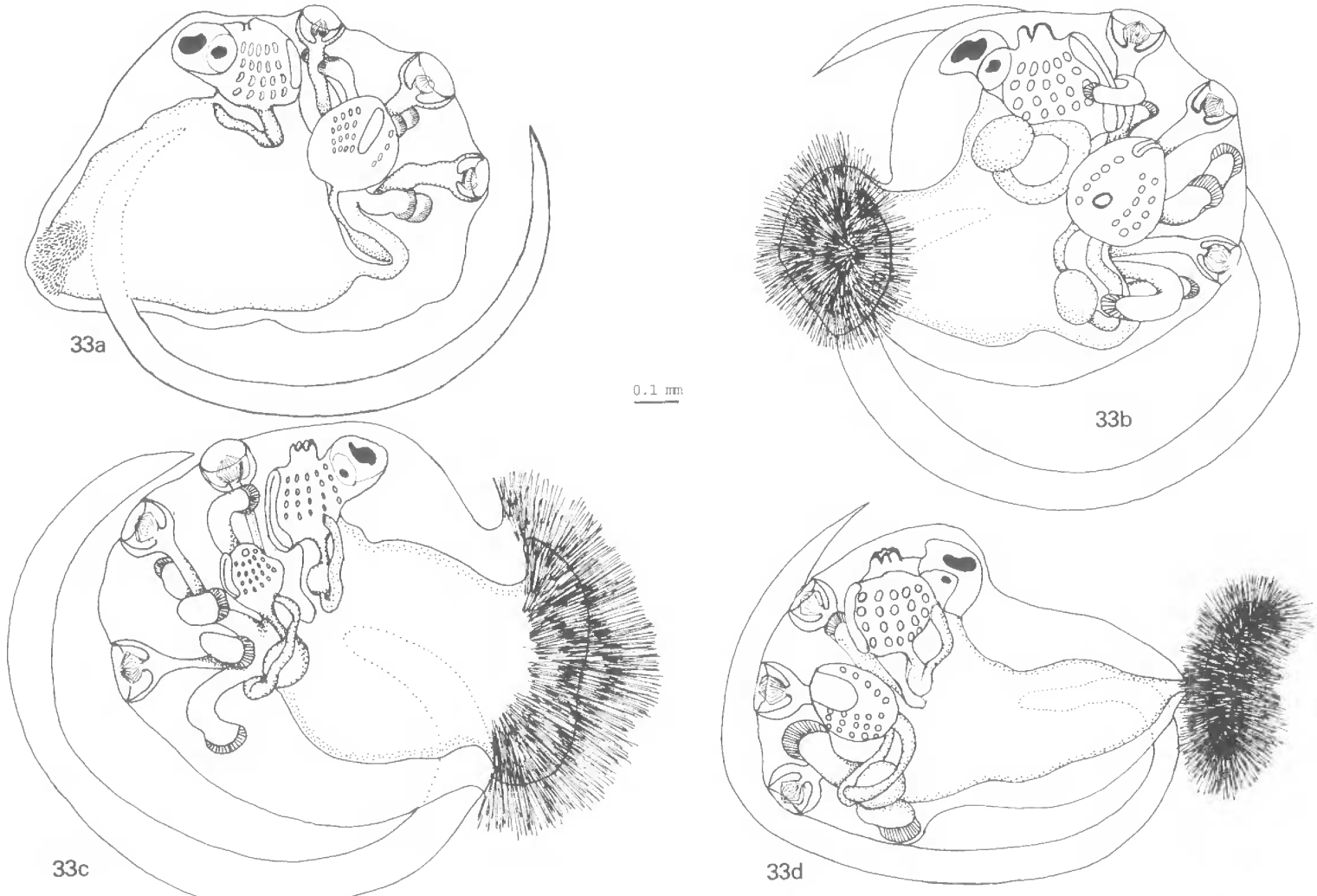



FIG. 33: *Diplosoma similis* (QM G9883) — larva showing development of rastrum (a, ectoderm cells project from postero-dorsal swelling of posterior haemocoelic chamber; b, c, rastrum is constricted off from remainder of larval trunk, hairs develop; d, arc shaped rastrum with upturned horns connected to larval trunk by a narrow neck, posterior end of larva narrows).

extends beyond the surface to which it is fixed until it attaches to an adjacent surface. Its capacity to bind rubble together results from this growth pattern that enables it to span the spaces between adjacent surfaces. The basal test is uneven and is often thickened where it fills in the irregularities in the surface to which it is attached. The colour of the living colony is very variable and may be almost any shade of dark, almost navy blue, bright green, or a whole range of teal or turquoise blue colours. The colonies at Heron I. are invariably green with patches of irridescent blue on the surface. Further to the north green colonies still occur but colonies of various shades of blue occur more often. At Low Is blue colonies of this species are the most common ascidian of the reef flat (I. Bennett, pers. comm.). In preservative the colonies become brownish green to grey as the plant cells lose their colour, and are themselves lost from the open common cloacal cavity. The test is translucent and without any other pigmentation. It is firm and gelatinous, but is not hard or tough, and is easily torn. The cloacal apertures are inconspicuous and sessile. The surface layer of test occupies about one third of the thickness of the colony, with a superficial layer of bladder cells. The anterior ends of the zooids are embedded in this surface layer. The common cloacal cavity is open, surrounding the test connectives that enclose the zooids between the surface and basal test. Zooids are not clumped together to any extent and are often suspended in the cloacal cavity by individual strands of test. Around the borders of the colony especially the common cloaca does not extend posterior to the zooids, and the abdomens are embedded on the basal test. In the centre of larger colonies, however, the cloacal cavity is more extensive and extends posterior to the zooid around the base of the long test connectives. Normally the cloacal cavity and the basal test each occupy about one third of the thickness of the colony, except where the basal test is thickened to accommodate irregularities in the substrate (see above). In some colonies there are clouds of an opaque white or brown particulate deposit in the test.

ZOOIDS: Zooids are 1 mm long. They are very evenly spaced in the test. The gut is at right angles to the thorax and there is a moderately long oesophageal region. The branchial siphon is well developed with a conspicuous sphincter muscle and 6 triangular branchial lobes. There is a moderately long prepharyngeal region. The atrial aperture is wide exposing most of the branchial sac. There are 4 rows of 6 round to oval stigmata. There is a fairly long retractor muscle that usually extends beyond the posterior end of the body. It is free from the body from a point near the branchial sac. There are stolonic vessels with the usual terminal ampullae projecting from the abdomen into the basal test. There are up to two sets of blastozooids. The body wall over the gut loop usually contains brown pigment although this is often lost in preservative. Occasionally the whole body wall of the zooid contains brown pigment. The abdomen is usually bent at an angle to the thorax from the base of the oesophagus. The stomach is especially long and roomy and gradually narrows at the pyloric end. It occupies almost the whole of the proximal limb of the gut loop. There are two ♂ follicles and the vas deferens is straight.

LARVAE: These are present in the larger colonies in July, February, December, and March and there is no indication of seasonal breeding. They are large, 0·8 mm long, excluding the posteriorly projecting rastrum or plant rake. The tail is wound three quarters of the way around the larval trunk. There is an oozooid with otolith and ocellus, and a single blastozooid. There are 3 pairs of slender ectodermal ampullae, each with modified columnar cells forming a swelling at the free end. The ectodermal ampullae branch off either side of the frontal stalk that supports the three median adhesive organs. In the mature larva, there is a deep division between the oozooid and the blastozooid. The latter remains associated with the frontal stalk. There are many larvae present in the common cloacal cavity that display a fully developed rastrum (see above, *D. virens).*

REMARKS: The species is distinguished from *Diplosoma virens* principally by the form and size of the colony, the simple two dimensional common cloacal system and absence of the conspicuous protruding cloacal apertures. The colony is less solid than that of *D. virens* and the plant cells are completely lost from the common cloacal cavity much more readily. The branchial sac is larger than in *D. virens*. The dark pigment in the body wall of the zooids is also characteristic of the present species — although it has often completely disappeared in the preserved material. The stomach is long and roomy and occupies almost the whole of one limb of the gut loop. The larvae of the two species are also similar and can be distinguished only by three pairs of ectodermal ampullae in the present species and a better

developed rastrum. The synonymy of specimens previously assigned to *D. virens* with *D. similis* Sluiter, is based on the consistency, the thickness and colour of the colony and the size and form of the zooids, the gut loop and the branchial sac.

The synonymy of *D. midori* (Tokioka 1954) was suggested by Eldredge (1967). The pyloric end of the stomach is more enlarged than in the present species. The retractor muscle of *D. midori* is shorter and more delicate, and the thoracic musculature is also more delicate than in the present species.

**Diplosoma midori** (Tokioka, 1954)
(Figs. 34, 35)

*Leptoclinum midori* Tokioka, 1954, p. 11.

MATERIAL EXAMINED

NEW RECORD: Tonga: coral reef, LWM, coll. R. Lewin, 17.4.76 QM G12669

DISTRIBUTION

RANGE: Japan: Tokara Is. (Tokioka 1954). Tonga (new record).

HABITAT: The species is taken on coral reefs.

DESCRIPTION

COLONY: A single colony is available. It is an irregular sheet 4 cm in maximum extent and up to 5 mm thick. Part of the border projects as a free lamella with thick internal test and a layer of zooids on both sides and around the border. The test is gelatinous and translucent, the zooids showing as dark and whitish points. The surface layer of test is very thin indeed. The zooids are contained in test connectives that cross the cloacal cavity joining basal to surface test. The basal test is very thick. Here and there the surface test is produced into protruding common cloacal apertures. The plant cells are contained in the common cloacal cavity.

ZOOIDS: The zooids are evenly distributed. They are about 1·5 mm long. The branchial opening is almost sessile and muscles are very inconspicuous. The retractor muscle is very fine and short. There are 4 rows of 6 delicate oval stigmata. The thorax is delicate. The gut loop is relatively short and slightly flexed ventrally. The stomach is long and roomy and occupies the whole length of the proximal limb of the gut loop. There are two ♂ follicles. The abdominal body wall of the preserved specimens is darkly pigmented.

LARVAE: These are 1·6 mm long. The tail is wound only one third of the distance around the larval trunk. There is a single blastozooid and the rastrum is especially well developed in the mature embryoes. In a few specimens the proximal end of the tail is withdrawn into the haemocoelic chamber of the left rastral horn. This may be an artefact resulting from the fixation and preservation of the colony. There are the usual 3 adhesive organs and 4 pairs of long slender ectodermal ampullae with modified terminal cells.

REMARKS: The species is distinguished from *D. similis* and *D. virens* by the very thin surface test, sessile branchial aperture, very delicate thorax and short fine retractor muscle. The zooid is distinguished from that of *D. multipapillata* by its delicate collapsible stigmata and the long roomy stomach. The colony of the present specimens is also distinctive in its double sided lamellae, that project free from the colony. In this it bears some resemblance to *Diplosoma perspicum* Sluiter, 1909 (> *D. translucidum* Hartmeyer, 1919). No plant cells have been located in the latter species which is further distinguished by its long, narrow stigmata. The free lamellae have not been described for the Japanese specimens, many of which were small colonies. It is most probable that there is considerable variation in this character, however, as there is in *Diplosoma virens* (above).

The 4 pairs of ectodermal ampullae distinguish the larvae from these of all other species.

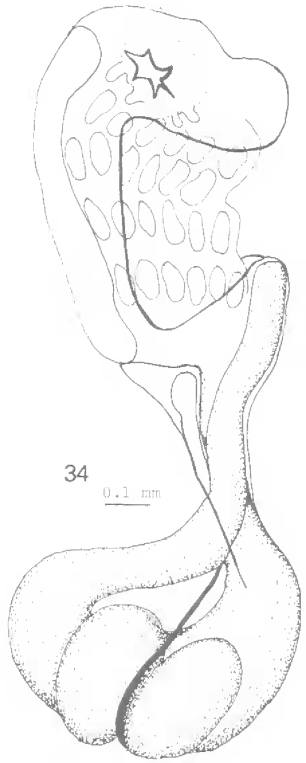
**Diplosoma multipapillata** n. sp.
(Figs. 36–39)

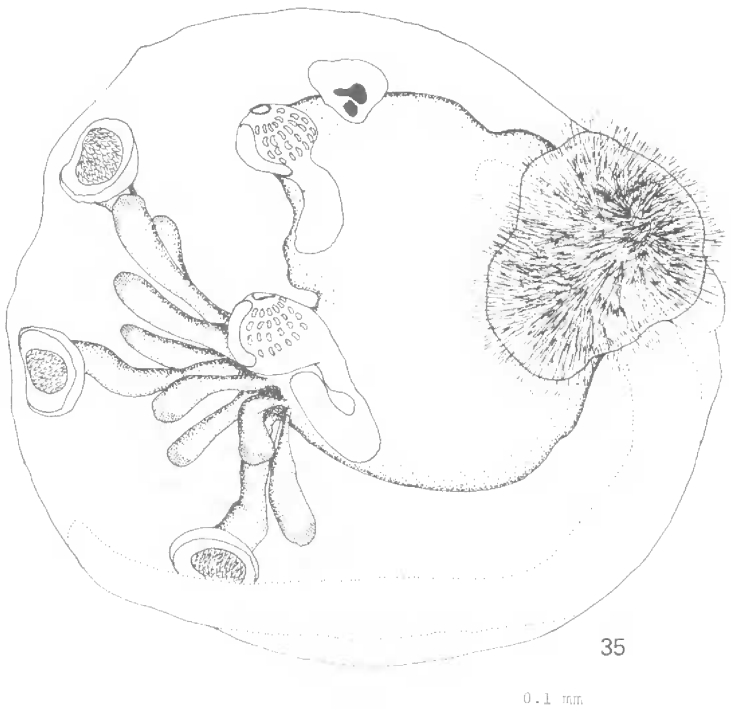
MATERIAL EXAMINED

NEW RECORDS: Malevu, Viti Levu, Fiji: fringing reef, close inshore, under cascades, coll. PK, 11.7.79. Holotype: QM G12487, Paratypes: QM G12488.

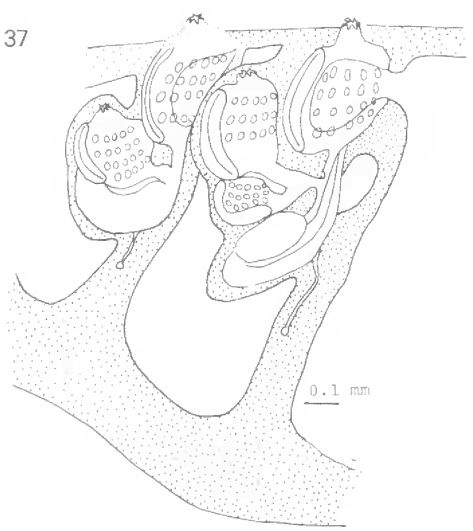
DISTRIBUTION

RANGE: The species has been taken only from the type location, where it is prolific and conspicuous.



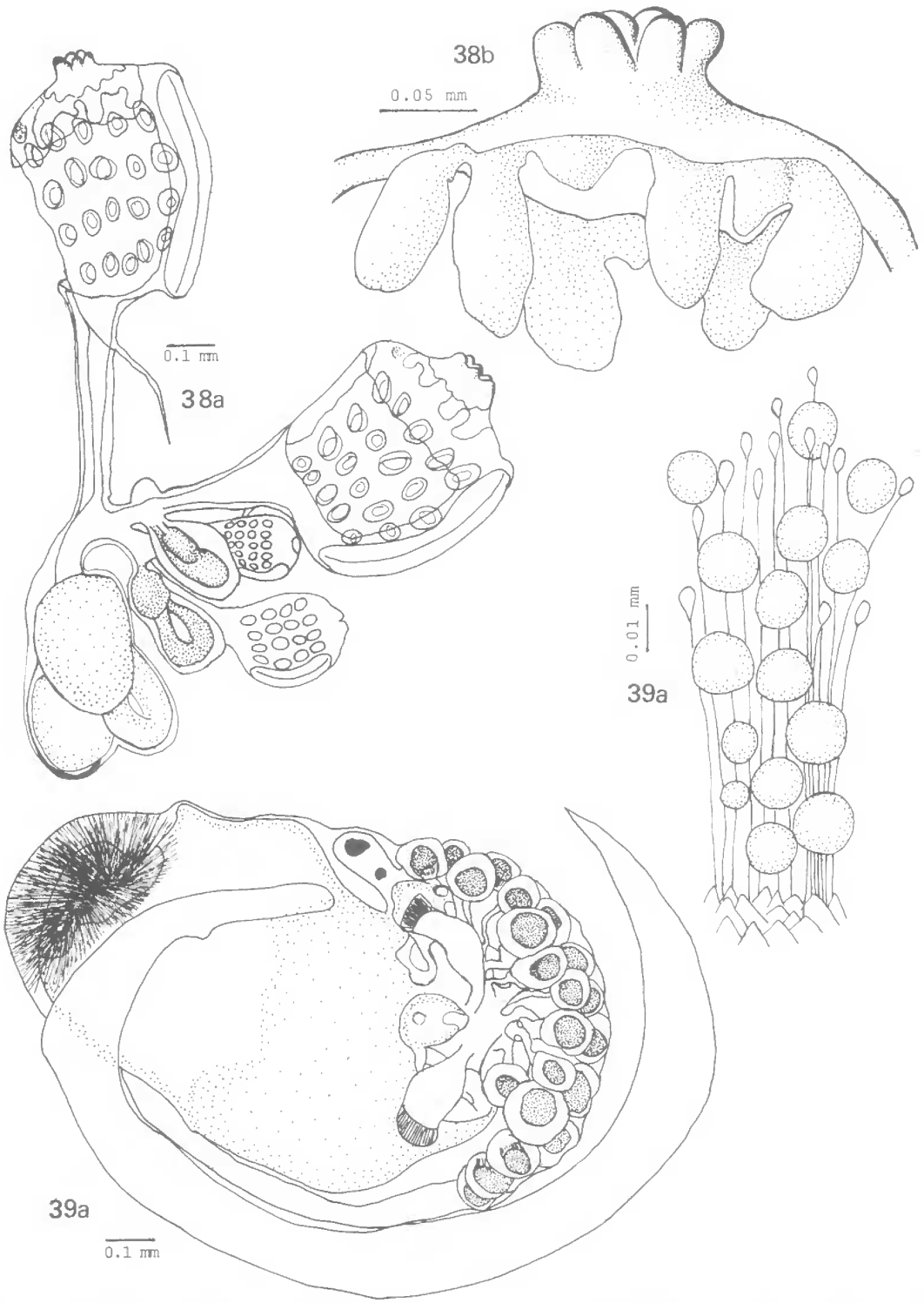








FIGS. 34–35: *Diplosoma midori* (QM G12699) — 34, zooid; 35, immature larva.

FIGS. 36–37: *Diplosoma multipapillata* (QM G12487) — 34, colony, upper surface; 35, cross section through colony.




FIGS. 38–39: *Diplosoma multipapillata* (QM G12487) — 36, zooid (a, zooid with blastozooids; b, branchial aperture and tentacles); 37, larva (a, whole larva; b, rastral hairs entangling algal cells).

HABITAT: It occurs close inshore, along the secondary or riverine rim of the fringing reef where it is bissected by the river channel that extends at right angles from the shore. The small colonies lie in profusion on the surface of the algal mat that covers this riverine rim and extends for a short distance down the upper gently terraced riverine slope. Here the waters of the reef flat drain into the river channel from about mid tide when the crest is exposed. The habitat is therefore swept by fast undirectional cascades of reef flat water for about half of each tidal cycle.

There are similar cascades of reef flat water into river channels at other points along the south western fringing reefs of Viti Levu but the species apparently occurs only at Malevu.

The habitat is a stringent one, and the species appears to be isolated in it (see below, Remarks).

## DESCRIPTION

COLONY: The colonies are a brilliant blue colour. In preservative this fades to a dull green, and later green-brown. Colonies are seldom more than 1 cm long, and are roughly elongate, elliptical, oval or irregular. They are about 1·5 mm in maximum thickness. The borders of the colony and parts of the basal surface are produced into branched holdfasts. The shape of some of the colonies suggests that they are lobulating. There is only a very narrow clear area around the border, the remainder of the surface being the brilliant blue of the plant cells lining the cloacal cavity. The whitish ampullae of the stolonic vessels from peripheral zooids are conspicuous in this translucent border.

The surface and the basal test are especially thin and the common cloacal cavity is very extensive, and is crossed by zooids embedded in individual test sheaths. The common cloacal apertures are on fairly long narrow cylinders that are bent to lie horizontally across the upper surface. Their upper rim is often incised in a deep V that extends back along the upper surface of the tube.

ZOOIDS: Zooids are crowded in the colony. They are about 0·8 mm long. There is no branchial siphon and the aperture is sessile, with 6 rounded lobes. There does not appear to be a sphincter muscle. The ring of 6 large and rather swollen branchial tentacles that alternate with shorter ones is just inside the aperture. The prepharyngeal area is narrow. There are 4 rows of 5 absolutely circular stigmata with relatively small openings. The cells lining the stigmata are deep and the pore is actually a short cylinder through the gut wall. The circular diameter of the pore is firmly maintained, tending also to maintain the branchial sac in a fully expanded condition. The atrial apertures are wide exposing all of the branchial sac. There are 3 and sometimes 4 sets of oesophageal blastozooids. There is a short, slender retractor muscle with very few fibres. The oesophageal neck is very long. The gut is bent at a slight angle to the thorax. Although most colonies contained larvae, there were no mature ♂ follicles and it is assumed that they were spent. There appears to be a single ♂ follicle. The vas deferens is straight, its proximal end hooked around the posterior border of gland.

LARVAE: These are large, about 1·3 mm long. The tail is wound almost all the way around the mid line of the trunk. On the right side of the anterior end of the larva there is a swelling from which 30 separate adhesive organs develop. In the mature larvae these spread out over the front. There is an oozooid with an ocellus and otolith and a single blastozooid. There are 3 pairs of long ectodermal ampullae with especially large columnar cells over the free end. The rastrum (see *D. virens,* above) develops from the postero-dorsal part of the larval trunk, just above the base of the tail as in *D. virens*. There is a deep furrow that develops in the larval ectoderm and test, around the rastral area. In due course, this is separated from the larval trunk as an inflated horizontal arc with upturned horns that lies transversely across the posterior end of the trunk supported by a narrow median stalk. The central cavity of the rastrum is in continuity with the posterior haemocoelic chamber. The rastral hairs are thick and stronger than those of *D. virens* and appear to become less tangled. They clearly differentiate from the larval test in this region, and they appear to be associated with the enlarged overlapping ectodermal cells of the rastrum. The exact details of the relationship between the ectoderm, the test and the rastral hairs will be determined through histological studies that are beyond the scope of the present work. Before metamorphosis the posterior end of the larval trunk narrows, and the rastrum, with the plant cells gathered from the parental cloacal cavity, is drawn inwards, partly by the overgrowth of the larval test, and partly by

the withdrawal of the posterior haemocoelic chamber, as the tail is drawn in, prior to its resorption.

REMARKS: The species is clearly most closely related to *D. similis* through its two dimensional cloacal cavity, well developed larval rastrum and ectodermal ampullae. The colonies superficially resemble those of *D. virens* but they are much flatter. The species is most clearly distinguished from both by its extraordinary larval adhesive apparatus. Adhesive strands of test that often form a continuous fringe around the borders of the colony are also much more conspicuous than in *D. virens*. The cylindrical cloacal apertures lying across the upper surface in the direction of the current flow are also a feature that sometimes occurs in *D. virens* but is more consistent and conspicuous in the present species. The prolific vegetative blastozooid production that is associated with proliferation of the colonies through lobulation, the sessile branchial aperture and large tentacles, the reduced musculature and very short, slender retractor, the small circular cylindrical stigmata and inflated thorax are also distinctive. The adaptive characters that distinguish this species from others are consistent with the requirements of its stringent habitat and suggest a possible explanation for its isolation and speciation.

The adaptations are those that enable the colonies to effect and maintain rapid and firm attachment to the substrate, to maintain their population density for sexual reproduction (Kott 1974) and to accommodate the fast unidirectional current that flows over them for about half of each tidal cycle (while the salinity in this inshore extent of the river channel is at its lowest). Thus, it is possible that the river provides the barrier to dispersal of those larvae that have not effected immediate fixation following their release from the parent colony. This barrier could be effective only if larvae are not released when the tide rises above the reef crest and the freshwater runoff from the river is minimal. This requirement would be satisfied if larvae are released through the narrow cloacal aperture only when a strong current flows over the surface of colony. No data are available at present to support this hypothesis. However the release of larvae on ebbing spring tides is known for many marine species (Johannes 1978) and enhances selection for free swimming larvae to maintain gene flow in tropical waters (Kott 1974). Such a stimulus to larval release, if it is present in this species, would have resulted in its isolation in the unique conditions that prevail.

## CONCLUSIONS

### PHYLOGENY

The characters of zooids and larvae of plant-bearing ascidians are summarised in Table 1. It will be seen that there are certain characters common to the groups of species in each genus. Species in the genus *Diplosoma* show the closest affinity with one another and differences are principally found in the larvae and colonies. It is probable that the capacity to accommodate algal symbionts occurred only once in this genus, and that speciation occurred only after the algal/ascidian relationship had been established.

Distinguishing characters between species in each of the genera *Tridemnum, Lissoclinum* and *Didemnum* do not indicate such close affinities and there is no clear indication regarding the origin of the algal symbiosis.

It is likely that a capacity for algal symbiosis was selected for separately in each of the species of *Didemnum* that demonstrate the phenomenon. *Lissoclinum voeltzkowi, L. bistratum,* and *L. patella* may represent a sister grouping having in common relatively large zooids, deeply invaginated lateral organs, larval blastozooids and similar ectodermal ampullae. *Lissoclinum punctatum* and *E. triangulum* share some adult characters with other *Lissoclinum* spp., but their larvae are different and do not suggest a relationship either with one another or with the other three species. Thus, the algal-ascidian symbiosis may have evolved on two separate occasions in *Lissoclinum* and again in *Echinoclinum*.

In *Tridemnum* the situation is confusing. The close relationships between adult zooids of *T. paracyclops* and *T. cyclops* are not supported by either the larvae or the respective methods of algal transfer. Further, although *T. clinides* differs markedly from others in the group in several respects, it does have the same mechanism of algal transfer as do *T. miniatum* and *T. cyclops*. At this stage an hypothesis that the unique method of algal transfer found in these species has been inherited from a common ancestor seems most convenient. If this hypothesis is accurate, speciation in *T. clinides, T. miniatum* and *T. cyclops* did not affect their plant transfer mechanism. In *T. paracyclops* however, isolation and speciation from *T. cyclops,* with which it shares many larval and adult characters, would have to have involved changes in the plant carrying capacity of the larvae that could be associated with its increased size. The larva of *T. strigosum* is the only one in which the plant cells are deeply embedded in the test.

GEOGRAPHIC RANGE

From Table 2, it can be seen that a range in the Indian and West Pacific Oceans is not unusual. It is also clear that records are far from complete at most locations: the majority of the widely ranging species are recorded from both the Great Barrier Reef and Fiji. It is likely that further surveys will show that a more comprehensive catalogue of species will be present over a great part of this region and that an extended range will be demonstrated for some of the species that appear at present to be relatively restricted. Habitats for some of the more common species are summarized in Table 3.

Latitudinal effects on habitat are especially evident for species that occupy exposed reef flat locations at low latitudes. *Lissoclinum voeltzkowi, Tridemnum cyclops, T. miniatum, Diplosoma virens* and *D. similis* all occur at Heron I. in cryptic habitats below low water mark near the edge of the reef. Here light values are considerably less than those they would encounter in the exposed habitats they usually occupy. It is possible that in this southern extent of their geographic range a greater diurnal temperature range on the reef flat may preclude their normal occurrence. *L. voeltzkowi,* however, only occurs occasionally at Heron I. and its range may be

TABLE 1. SUMMARY OF CHARACTERS OF ALGAL-BEARING DIDEMNIDS OF THE INDO-WEST PACIFIC*

| | ZOOIDS | | | | | | | | | | COLONY | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Branchial lobes** | Atrial aperture | Retractor muscle | Gut loop | ♂ follicles | Vas deferens spirals | Size (mm) | Endostylar pigment cap | Lateral organ | Stigmata | Number of systems/colony*** | Spicules (u): spherical (sp), Stellate (st), flattened (fl) | Plant cells:* |
| *Didemnum* | | | | | | | | | | | | | |
| *molle* | 6 | wide | long | long | 1 | 6½ | 1·5 | — | shallow | 8 long | 1 | 5–15 sp | CC |
| *viride* | 6 | wide | medium | long | ? | ? | 0·7 | — | shallow | 5 oval | >1 | 30–40 st | E |
| *Tridemnum* | | | | | | | | | | | | | |
| *clinides* | 6 | *siphon* | *short* | medium | 1 | 6½ | 1·0 | none | shallow | 5 long | 1 | 30–40 st | *E* |
| *miniatum* | 6 | transverse | medium | medium | 1 | 5½ | *0·8* | none | shallow | 7 oval | 1 | *10–20 sp* | *E* |
| *strigosum* | 6 | transverse | long | medium | 1 | 6½ | *0·5* | none | projects | 7 oval | >1 | *50–80 st* | *E* |
| *nubilum* | 6 | transverse | medium | medium | 1 | 5½ | *0·6* | none | projects | 5 oval | >1 | *30–50 sp* | *E* |
| *cyclops* | 6 | transverse | long | medium | 1 | 5½ | 1·5 | *present* | shallow | 7 long | 1 | 40–60 st | CC |
| *paracyclops* | 6 | transverse | medium | medium | 1 | *9½* | 1·5 | *present* | shallow | 7 long | >1 | 30–80 st | CC |
| *Lissoclinum* | | | | | | | | | | | | | |
| *voeltzkowi* | *2* | wide | *none* | *short* | 1 | — | 0·8 | — | *deep* | 8 medium | 1 | 20–40 st | CC |
| *bistratum* | *2* | wide | *reduced* | *short* | 1 | — | 0·9 | — | *deep* | 8 long | >1 | 30–50 sp | CC |
| *patellum* | *2* | wide | *none* | *short* | 1 | — | 3·0 | — | *deep* | 14 long | >1 | 10–80 sp | CC |
| *punctatum* | 6 | wide | *none* | *short* | 1 | — | 1·0 | — | *deep* | 8 long | >1 | 10–30 sp | CC |
| *Echinoclinum* | | | | | | | | | | | | | |
| *triangulum* | 6 | wide | *none* | *medium* | 1 | — | 1·4 | — | *deep* | 12 long | >1 | *30–80 fl* | *E* |
| *Diplosoma* | | | | | | | | | | | | | |
| *virens* | 6 | wide | long | long | *2* | — | 1·0 | — | none | 5 oval | 1 | — | CC |
| *similis* | 6 | wide | long | long | *2* | — | 1·0 | — | none | 6 oval | >1 | — | CC |
| *midori* | 6 | wide | *short* | medium | *2* | — | 1·5 | — | none | 6 oval | 1 | — | CC |
| *multipapillata* | 6 | wide | *short* | long | *1* | — | 0·8 | — | none | *5 round* | 1 | — | CC |
| *handi* | 6 | wide | *short* | long | *1* | — | 1·0 | — | none | 6 oval | 1 | — | CC |

* Those characters that may be considered diagnostic of a species or of groups of species appear in italics.

** A branchial siphon is present, except in *D. multipapillata* and *D. midori* where the aperture is sessile.

*** Colonies that form extensive sheets have >1 system; those with single systems may lobulate and divide to maintain the characteristically small sized colonies.

restricted by lower light levels at higher latitudes. Records show that of all the reef flat species, *L. voeltzkowi, L. bistratum* and *T. cyclops* have the greatest range in both oceans. Of these, *L. voeltzkowi* which normally occurs in the most exposed locations on the reef flat is most restricted latitudinally.

*L. bistratum* has the greatest latitudinal range of the reef flat species, its southern limit being off south eastern Queensland and its northern limits at the Tokara Is and the Red Sea. *Diplosoma virens* and *D. similis* have a similar recorded east-west range in both oceans. Although neither is known to extend west of Sri Lanka at present, *D. similis* is the only plant-bearing species known from Hawaii. The reef slope species *D. molle* and *L. patellum* also occur in both oceans. They are both common at Heron I. and are also known from Cockburn Sound. The former is also recorded from Okinawa and its latitudinal range is as extensive as that of *L. bistratum*. *Didemnum viride* (Ceylon and Madagascar) and *Tridemnum paracyclops* (Great Barrier Reef) have more resctircted ranges and only *Tridemnum strigosum* and *T. nubilum* (Philippines), *Diplosoma multipapillata* (Fiji), and *D. handi* (Caroline Is.) are endemic.

TABLE I (cont.)

| | LARVAE | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Ectodermal cups | Adhesive organs | Ectodermal ampullae | Modified ectodermal cells on ampullae | Blastozooids | Yolk mass†† | Plant cell transfer | Size (mm) | Distribution††† |
| *Didemnum* | | | | | | | | | |
| *molle* | *deep* | 3 | 2 prs | none | *2* | posterior | posterior barrel | 0·9 | IWP |
| *viride* | ? | ? | ? | ? | ? | ? | ? | ? | WI |
| *Tridemnum* | | | | | | | | | |
| *clinides* | medium | 3 | 3 prs | none | none | anterior | *trunk encased* | 0·6 | WP |
| *miniatum* | medium | 3 | 3 prs | none | none | anterior | *trunk encased* | 0·7 | WP |
| *strigosum* | medium | 3 | 6–8 prs | none | none | anterior | *embedded* | *1·1* | E(P) |
| *nubilum* | ? | ? | ? | ? | ? | ? | ? | ? | E(P) |
| *cyclops* | medium | *2* | 2 prs | none | none | anterior | *trunk encased* | 0·5 | IWP |
| *paracyclops* | medium | *2* | *4½ prs* | none | none | anterior | *posterior cap* | 1·0 | GBR |
| *Lissoclinum* | | | | | | | | | |
| *voeltzkowi* | medium | 3·2 | 8 prs | *present* | *2* | posterior | posterior cap | 1·5 | IWP |
| *bistratum* | medium | 3 | 8 prs | *present* | *2* | posterior | posterior cap | 1·0 | IWP |
| *patellum* | *shallow* | 3 | *15 prs* | *present* | 1 | posterior | posterior cap | *2·5* | WP |
| *punctatum* | medium | 3 | (?6 prs) | ? | (?none) | *anterior* | ? | 0·6 | WP |
| *Echinoclinum* | | | | | | | | | |
| *triangulum* | medium | 3 | 3 prs | (?present) | *none* | *anterior* | ? | 0·6 | WP |
| *Diplosoma* | | | | | | | | | |
| *virens* | medium | 3 | *2 prs* | present | 1 | posterior | rastrum | 1·0 | IWP |
| *similis* | medium | 3 | 3 prs | present | 1 | posterior | rastrum | 1·0 | WP |
| *midori* | medium | 3 | *4 prs* | present | 1 | posterior | rastrum | 1·5 | WP |
| *multipapillata* | *shallow* | *30* | 3 prs | present | 1 | posterior | rastrum | 1·3 | E(F) |
| *handi* | ? | ? | ? | ? | ? | ? | ? | ? | E(C) |

† E=embedded, cc=in cloacal cavity.

†† The position of the yolk mass is apparently related to the presence or absence of blastozooids.

††† IWP — Indo-west Pacific; WP — West Pacific; GBR — Great Barrier Reef; E (P,C,F) — Endemic (Philippines, Caroline Is, Fiji); WI — West Indian Ocean

TABLE 2: GEOGRAPHIC RANGE OF PLANT-BEARING DIDEMNID ASCIDIANS.*

| Species | Zanzibar 5°S | Malagasy 20°S | Red Sea 20°N | Sri Lanka 8°N | Indonesia 10°S | Darwin 10°S | Cockburn Sd 32°S | GBR 10 to 24°S | Mooloolaba 28°S | Borneo 0° | Philippines 10°N | Tokara Is 30°N | Okinawa 26°N | Palau Is 10°N | Eniwetok 10°N | Marshall Is 10°N | Hawaii 20°N | Gilbert Is 0° | Line Is 0° | Fiji 20°S | Tonga 23°S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *D. viride* | | X | | X | | | | | | | | | | | | | | | | | |
| *D. molle* | X | X | | | X | X | X | X | | | X | | X | X | | | | | | X | |
| *T. cyclops* | | X | | | | X | | X | | | X | | | | X | | | X | | X | |
| *L. voeltzkowi* | | X | | | | | | X | | | | | | | | | | | | X | |
| *L. bistratum* | | | X | | X | X | | X | X | | | X | | X | | | | | | X | X |
| *D. virens* | | | | X | X | X | | X | | | X | | | | | X | | X | | X | |
| *D. similis* | | | | | X | | | X | | | X | | | | X | X | X | | X | X | |
| *T. clinides* | | | | | | | | X | | | X | | | | X | | | | | X | |
| *L. punctatum* | | | | | | | | X | | | | | | | | | | | | X | |
| *D. midori* | | | | | | | | | | | | X | | | | | | | | | X |
| *L. patellum* | | | | | X | | X | X | | X | | | | X | | | | | | | |
| *L. triangulum* | | | | | X | | | X | | | X | | | | | | | | | | |
| *T. miniatum* | | | | | | | | X | | | X | | | | | | | | | | |
| *T. paracyclops* | | | | | | | | X | | | | | | | | | | | | | |

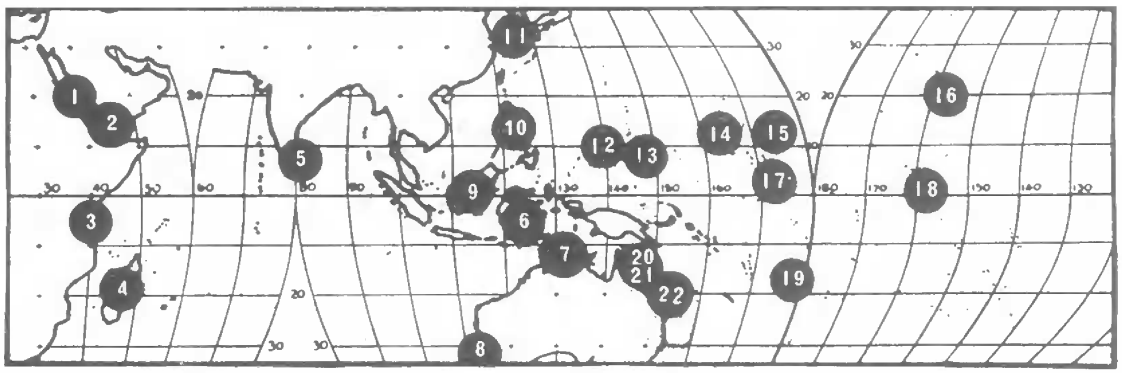
* Endemic species recorded from single geographic Locations only are not included.

The mechanism whereby these ubiquitous species avoid isolation and speciation is not known. Kott (1974) suggested that pelagic larvae are the means by which gene flow is maintained, despite opposite pressures to avoid dispersal. Crisp (1977) and Johannes (1978) have also discussed the role of the pelagic larvae of marine organisms. Where habitats are transient the role of the larvae to disperse and colonise is acknowledged. Yet it is in the tropics where habitats are not transient that sessile organisms with the free swimming larvae are most common. Johannes (1978) has explored an hypothesis that fish gametes and larvae are dispersed as a result of selective pressures imposed by predators in the parental shallow water habitats, and he has argued that some progeny are likely to be recruited back into the parent population by means of gyres or other circulatory patterns.

Crisp (1977) pointed out that dispersal *per se* is wasteful; and that adaptive advantages associated with it must therefore transcend opposite pressures to maintain populations. It is most unlikely that pressures to avoid wastage (through predators) would have caused the evolution of other strategies (such as those described by Johannes) that also promote dispersal and loss from the adult population.

TABLE 3: CHARACTERISTIC HABITATS OF REEF FLAT SPECIES AT LOW LATITUDES.

| Inner sandy reef flat | Outer sandy reef flat | Living coral zone, outer reef flat (with pools) | Rubble zone and Reef rim with surge channels, pools | Reef Slope |
|---|---|---|---|---|
| *T. miniatum*<br>*D. virens* | *L. voeltzkowi* | *L. bistratum*<br>*T. cyclops* | *D. similis*<br>*L. punctatum*<br>*T. clinides* | *L. triangulum*<br>*L. patellum*<br>*D. molle* |




1. Red Sea
2. Gulf of Tadjourah
3. Zanzibar
4. Malagasy
5. Ceylon
6. Indonesia
7. Darwin
8. Cockburn Sound
9. Borneo
10. Philippines
11. Tokara Is.
12. Palau Is.
13. Caroline Is.
14. Eniwetok
15. Marshall Is.
16. Hawaii
17. Gilbert Is.
18. Line Is.
19. Fiji
20. Lizard I.
21. Green I.
22. Heron I.

FIG. 40: Locations between Latitude 30°S and 30°N, and Longitude 30°E and 130°W where didemnids with prokaryotic symbionts have been recorded (see Table 2).

Therefore it seems likely that some advantage other than population maintenance must be associated with the existence of free swimming larvae. The length of larval life of the present species is not known. The condition of the developing adult organs and larval adhesive organs before their release from the parent colony do not suggest a long larval life. Further, the larvae are generally large and it is unlikely that their relatively short tails are especially effective swimming organs. The larvae do not appear to be ideal as vehicles for gene flow between very isolated populations (see also Crisp *loc. cit.*). Nevertheless, they appear to be the only vehicle by which gene flow can occur. Their recruitment through the chains of islands and reefs that exist around the Indo-west Pacific coralline region would explain the lack of endemism that is characteristic of this region. If they have been selected for in order to fulfil this role, it is probable that there are associated strategies that will ensure their maximum dispersal. The probability of larval release on ebbing tides when there is maximum water flow over the parent colonies is discussed above (see *Diplosoma multipapillata,* Remarks).

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Carlisle (1961) has observed metamorphosed colonies of *Diplosoma listerianum* either in mid water or attached to the surface film. Distribution of these species may therefore occur irrespective of the length of larval life.

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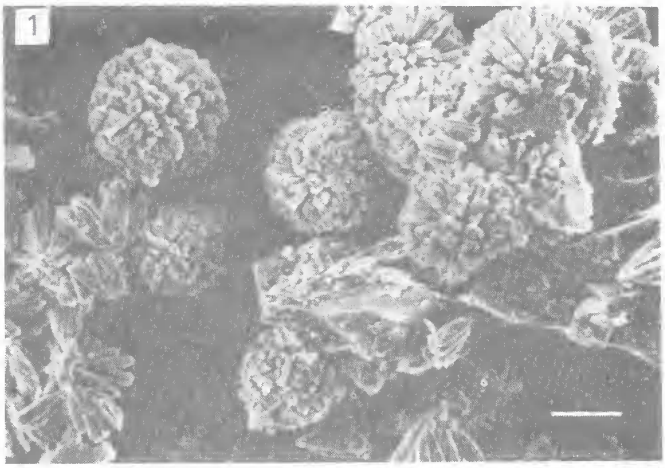
PLATE 1

1: *Didemnum molle,* spherical spicules with loose flat ended rays, 0·005–0·015 mm (scale 0·005 mm).

2: *Didemnum viride,* stellate spicules with few long pointed rays, 0·03–0·04 mm (scale 0·1 mm).

3a, b: *Lissoclinum voeltzkowi,* spicules stellate or spherical (with blunt ended rays), 0·02–0·04 mm (scale 0·05, 0·005 mm).

4: *Lissoclinum voeltzkowi,* living colonies (Green I.).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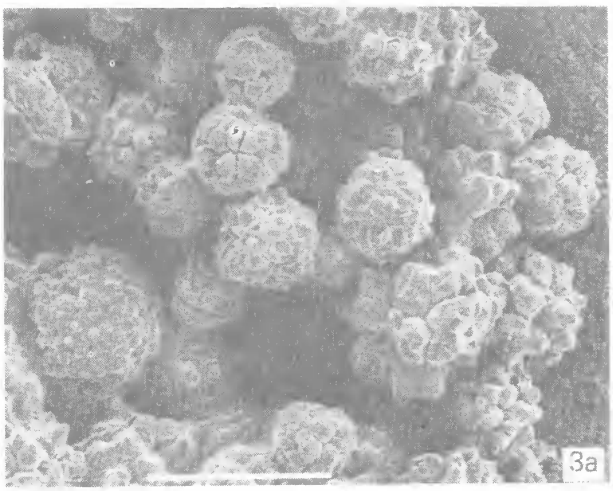
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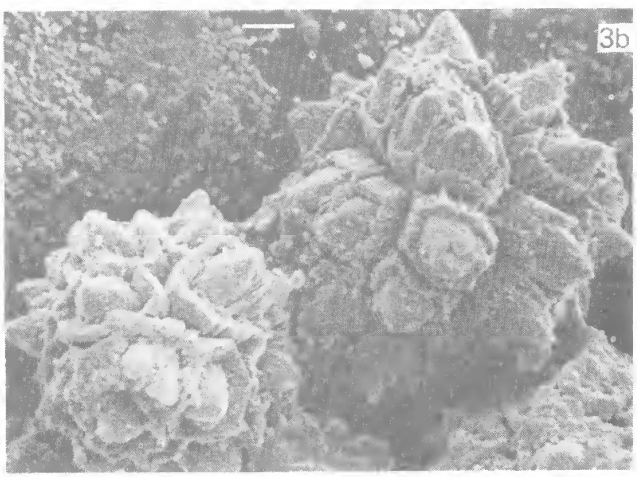
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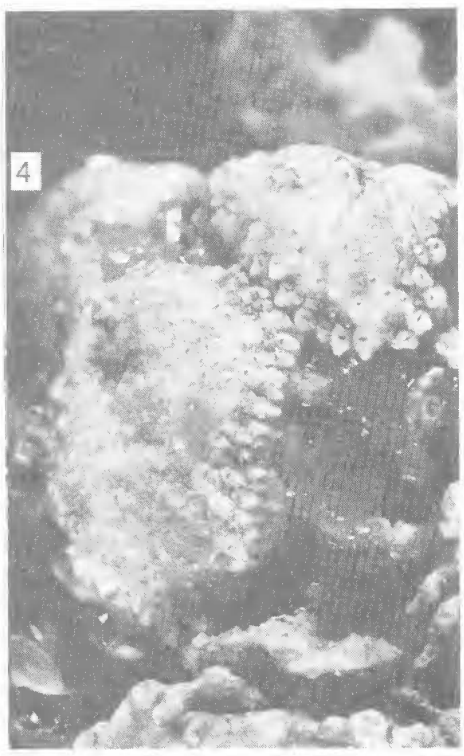
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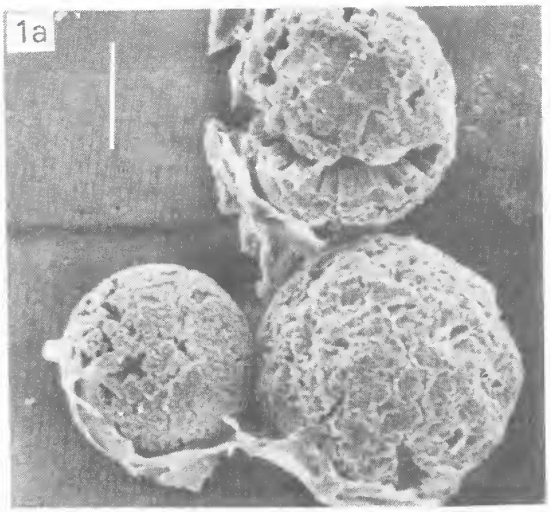
PLATE 2

1a, b: *Lissoclinum bistratum,* spicules spherical with tight blunt ended rays, 0·03–0·05 mm (scale 0·012 mm).

2: *Lissoclinum patellum,* spicules spherical with tight needle-like rays 0·01–0·08 mm (scale 0·005 mm).

3: *Lissoclinum punctatum,* spicules spherical, with slightly irregular needle-like rays, 0·01–0·03 mm (scale 0·005 mm).

4: *Echinoclinum triangulum,* spicules flat, triangular, square or trapezoid with loose needle-like rays of varying length, 0·03 to 0·08 mm (scale 0·005 mm).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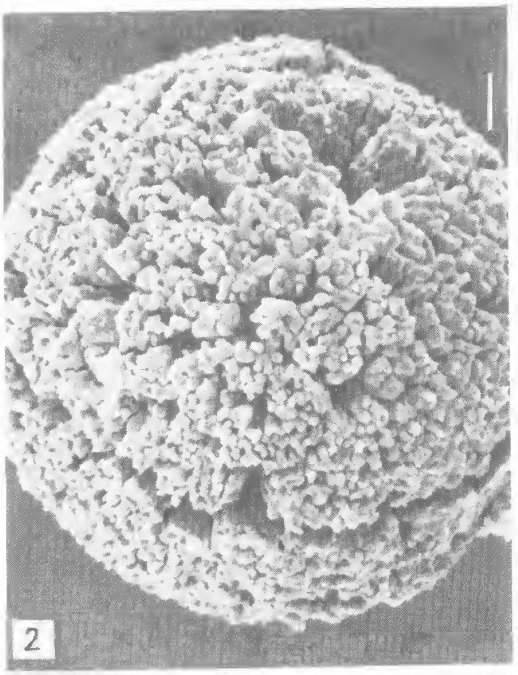
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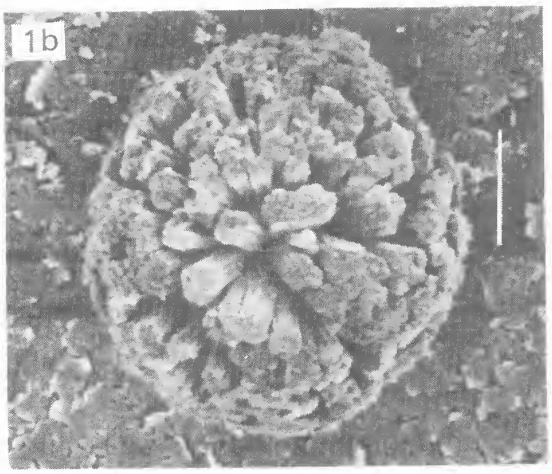
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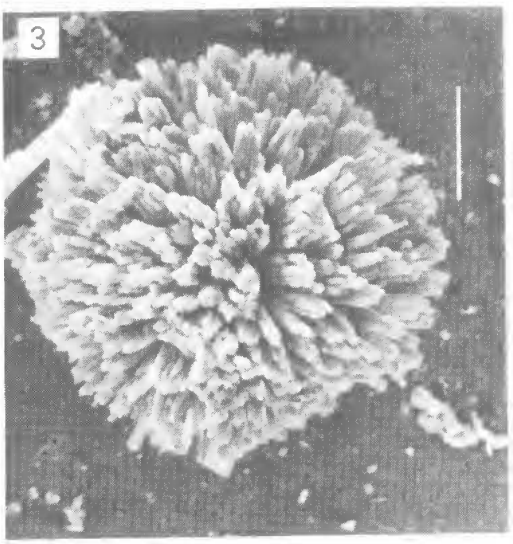
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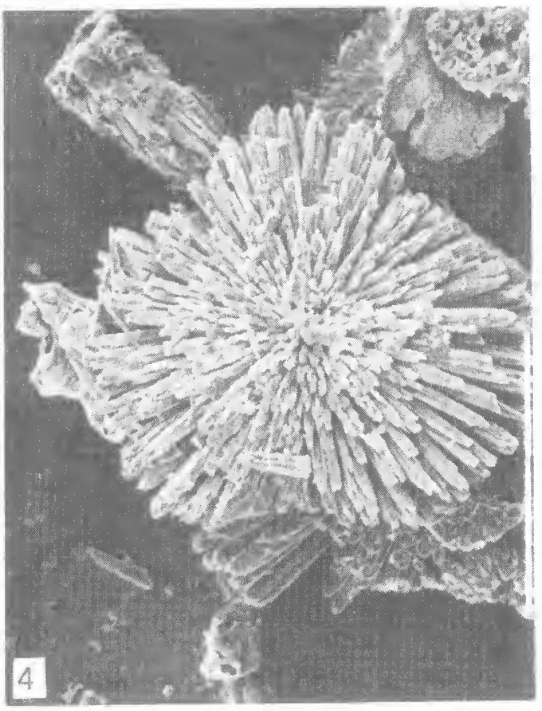
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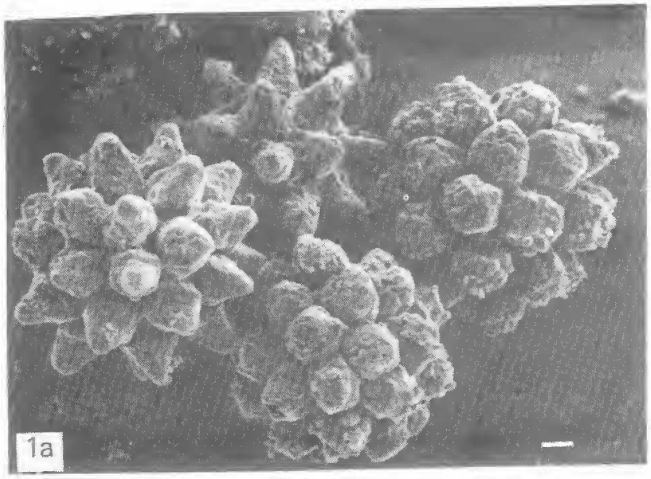
PLATE 3

1a, b: *Tridemnum clinides*, stellate spicules with rounded or conical rays, 0·03–0·04 mm (scale 0·005 mm).

2: *Tridemnum miniatum*, spherical spicules with loose flat ended rays, 0·01–0·02 mm (scale 0·005 mm).

3: *Tridemnum strigosum*, stellate spicules with few conspicuously projecting rays, 0·05–0·08 mm (scale 0·005 mm).

4: *Tridemnum nubilum*, stellate spicules with numerous short conical rays projecting, 0·03–0·05 (scale 0·01 mm).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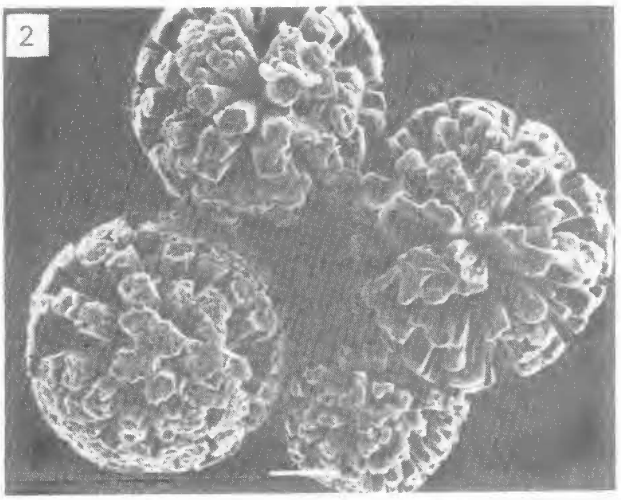
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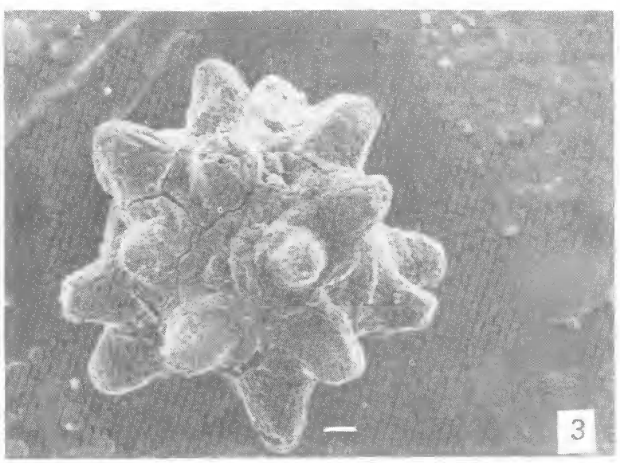
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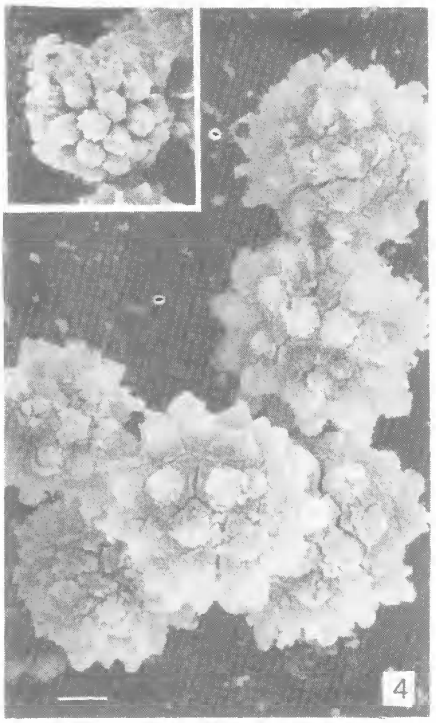
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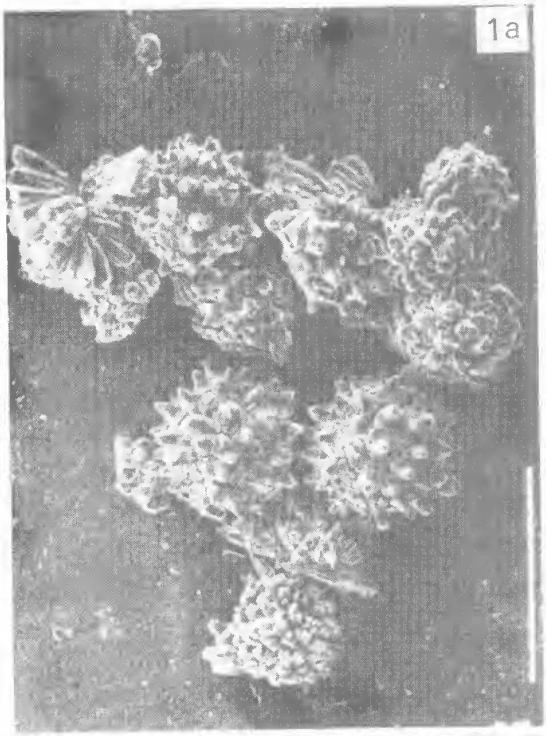
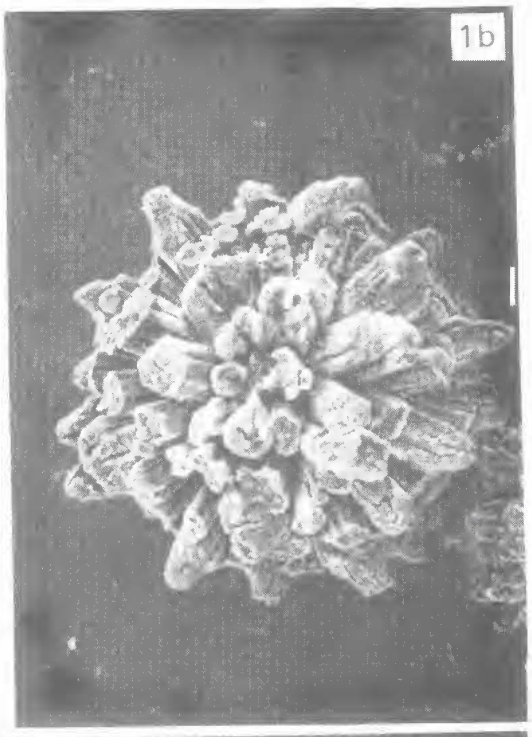
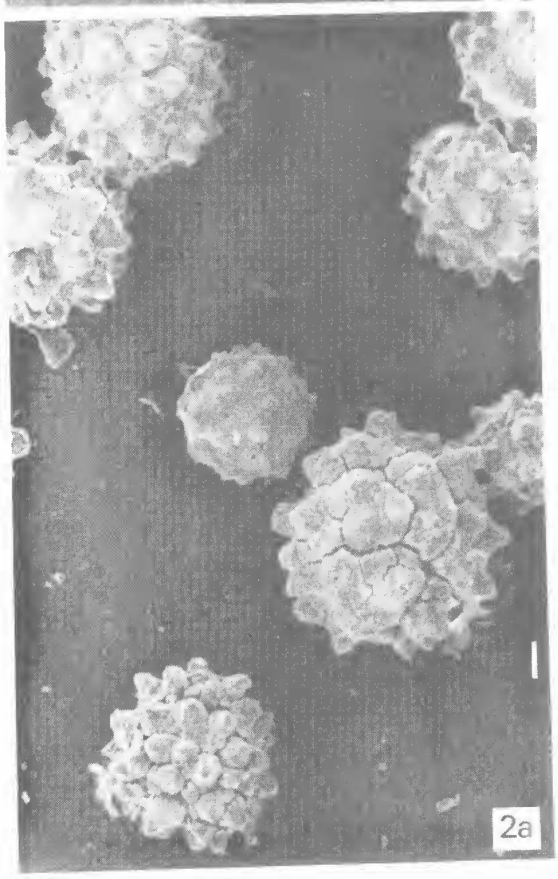
PLATE 4

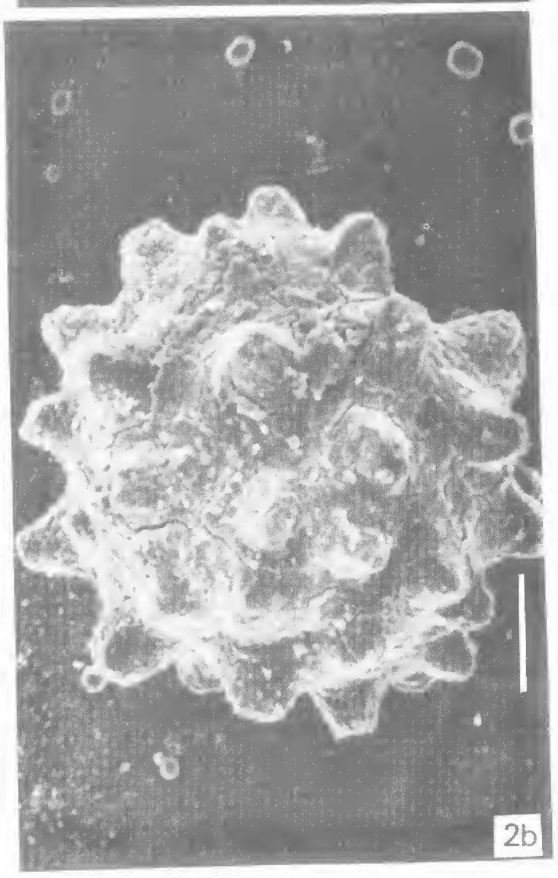
1a, b: *Tridemnum cyclops,* stellate spicules with conical or flat ended rays, 0·04–0·06 mm (scales 0·05 mm, 0·005 mm).

2a, b: *Tridemnum paracyclops,* almost spherical spicules with projecting conical rays, 0·03–0·08 mm (scale 0·011 mm).


1a


1b


2a


2b